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SPIDERS IN UNITED STATES FIELD CROPS AND THEIR POTENTIAL EFFECT ON CROP PESTS

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ABSTRACT

An analysis of 29 faunal surveys of spiders found in nine field crops in the United States indicates the presence of 614 species in 192 genera and 26 families. These species represent 19% of the ca. 3311 species occurring in North America. Five families included 61% of the species reported in field crops: Salticidae (89 spp.), Linyphiidae (78), Araneidae (77), Theridiidae (64), and Lycosidae (62). Considerably more species have been observed in cotton (308 spp.), soybean (262), and alfalfa (233) than in guar (52), rice (75), and grain sorghum (88). Intermediate numbers of species have been observed in peanuts (131), corn (136), and sugarcane (137). The North American spider fauna is estimated at the species level to be 59% web-spinners and 41% wanderers, while those reported from field crops are estimated to be 44% web-spinners and 56% wanderers. These differences may be attributable to guild characteristics associated with dispersal and ability to survive in disturbed habitats. The 42 most frequently occurring spider species were considered in detail and demonstrated that the active wandering guild comprised the largest portion (45%) of this group. Orb-web (21%), sheet-web (19%), ambush-wander (10%), and web-matrix (5%) spiders represented other guilds. The most frequently occurring species in field crops were *Oxyopes salticus* Hentz (Oxyopidae), *Phidippus audax* (Hentz) (Salticidae), and *Tetragnatha laboriosa* Hentz (Araneidae). These three species are prime candidates for augmentation and conservation in field crops or in adjacent habitats as part of a strategy to increase predation on crop pests.

INTRODUCTION

As recently as 1984, a review of spiders as biocontrol agents was able to lament the current failure to consider the potential of spiders in insect suppression programs (Riechert and Lockley 1984). This same review pointed out that generalist predators such as spiders can in certain situations limit exponential increases in insect populations in both natural and agricultural systems. A more recent review of an abundant spider in agroecosystems, *Oxyopes salticus* Hentz, indicated the considerable potential of this species for suppressing insect pest

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populations in agroecosystems (Young and Lockley 1985). These reviews and others increasingly point to the importance of spiders as part of a strategy of Integrated Pest Management.

Any investigator, however, who wishes to examine the spider fauna in a field crop faces an immediate problem. The identification of species is a tortuous process for the novice, and may be close to impossible for many taxonomic groups and for immature spiders. There is no single reference available to identify the approximately 3311 species in North America, and only one regional work (New England) attempts to provide identification aids for all resident species (Kaston 1981). The approximately 470 genera of spiders in North America can be identified with the aid of Roth (1985). The most commonly used North American identification manual for novices considers only 223 genera and, though presenting generalized descriptions of many species, contains no species-level keys (Kaston 1978). Thus the identification of spiders must be performed by (1) use of generic revisions of a highly technical nature, many of which are outdated, (2) comparison with reference collections, most of which are at major urban museums and relatively inaccessible to the agricultural researcher, and (3) consultation with an expert in spider taxonomy, the number of which may be less than 20 in the United States and Canada. Several of these experts are retired or nearly so; all are overworked and reluctant to process large lots of specimens. These factors alone may have discouraged past research in the spider fauna in agroecosystems; they continue to be impediments to present and future research. In this regard it is noteworthy that two agricultural research groups in the United States that actively publish surveys of field-crop spiders are fortunate to have in-house taxonomic expertise (i.e., Dean and Eger 1986, Lockley and Young 1986).

We have failed to detect significant movement in the last 10 years toward implementation of any pest suppression strategy in the United States that specifically includes spiders as part of the suppression strategy, though the TEXCIM model for cotton fleahopper-*Heliothis* suppression may be a recent exception (Hartstack and Sterling 1988). One possible reason for the slow progress may be due to minimal knowledge concerning the species composition, densities, and distribution of spiders in field crops. In an attempt to facilitate the use of spiders in insect suppression strategies, we here summarize 29 faunal surveys of spiders found in field crops of the United States. We further evaluate the quality of the data base, analyze and interpret the data, and suggest directions for future research.

MATERIALS AND METHODS

The entomological-araneological literature was searched for surveys of spiders in North American field crops. We restricted the database to surveys that included the following information: (1) majority of spiders identified to species, (2) degree of sampling effort specified, (3) method and diel period of sampling specified, and (4) degree of taxonomic assistance indicated. Information from items 2-4 was coded (Table 1) and placed as an annotation after each survey citation (Appendix 2). This format provided criteria to evaluate survey quality.

The nomenclatural problems associated with such a compilation from 29 different sources were particularly difficult to overcome. Many surveys contained

Table 1.—Summary of sampling methodologies utilized in 29 field-crop surveys of spiders. Values represent descriptive statistics or number in each category.

A. Number of years of sampling	Mode 3
Range 1-10	Below mean 18
Mean 2.7	Not indicated 3
Mode 1, 3	E. Methods of sampling
B. Maximum number of months sampled	1. Sweep 20
within a year	2. Vacuum 11
Range 3-12	3. Pitfall 18
Mean 6.2	4. Hand 16
Mode 4	5. Berlese 3
Not indicated 4	6. Dip net 1
C. Diel sampling period	7. Shake-cloth 7
1. Diurnal 29	F. Acknowledgment of taxonomic
2. Nocturnal 6	assistance
D. Maximum no. fields sampled/month	1. Yes 17
Range 1-40	2. No 12
Mean 8.8	

species names that: (1) recently had been split into several species, or combined with another species name, (2) were no longer valid, (3) belonged in a different family or genus, or (4) were probable misidentifications. The resultant species list is our best estimate of the correct names and placement of species. We followed Roth (1985) as the most current source of information on placement and acceptability of familial and generic names.

RESULTS AND DISCUSSION

Limitations of the data.—Most surveys of arthropods in field crops usually focus on a particular pest or group of pests (e.g., Scott et al. 1983a). When non-pest arthropods are collected they are typically recorded as “beneficials”, or the most common ones may be determined to species (e.g., Scott et al. 1983b; Parencia et al. 1980). This usually is not the case for spiders, which unfortunately are often lumped together into one group (e.g., Smith et al. 1976), or at best subdivided into functional groups (e.g., Lockley et al. 1979). Such generalized categorizations may be due to the identification problems previously mentioned and to the fact that arachnologists typically have not conducted faunal surveys in field crops, preferring more undisturbed areas where spider populations are usually larger and more diverse. The net result is a paucity of information about spiders associated with field crops. Nevertheless, we obtained copies of 29 surveys of field-crop spiders that met our criteria for inclusion. Only 12 of these surveys were published in refereed journals; the remainder appeared in state scientific societal or agricultural experiment station publications (12), or as unpublished theses and dissertations (5).

Assessing the quality of the 29 manuscripts utilized in one analysis was difficult, because established criteria for determination of quality were unavailable. Six parameters were chosen that we believe should be included when a faunal survey is published: (1) number of years of sampling, (2) maximum number of months sampled within a year, (3) diel sampling period, (4) maximum number of fields sampled per month, (5) method of sampling, and (6)

acknowledgement of taxonomic assistance. We then tabulated the manuscripts within categories of each parameter (Table 1).

One survey was conducted over a ten-year period, another over six, whereas 22 surveys lasted three years or less. Surveys <3 years are not likely to demonstrate long-term trends, but should be sufficient to detect most species in an area. Although several surveys were conducted over an entire 12-month period each year, a majority (17) lasted for only 3-6 months. In some cases this short time represented the life-span of the crop, though usually survey duration coincided with the period of crop maturity or with peak arthropod abundance. The number of different sites (fields) sampled each month ranged from 1 to 40; half the surveys included four or fewer sample sites. Small sample sizes may not detect variability within and among sites and may distort the relationship of single-site abnormalities to other more typical sites.

Considerable variability was apparent in the importance that investigators placed on sampling effort and the methods employed; some surveys even failed to mention sampling effort. Most surveys utilized a variety of collection methods, though five surveys used only one method. When methods to obtain both foliage- and ground-dwelling spiders were employed, total number of species obtained were higher than in single-strata surveys. Only six collection programs included methods that specifically obtained nocturnal specimens, though 18 programs included a method (pitfall) that collected ground-dwelling forms both day and night.

Twelve surveys failed to acknowledge taxonomic assistance from specialists. Given the aforementioned difficulties in spider identification, the likelihood that a non-specialist could correctly identify all specimens obtained in a faunal survey is indeed remote. Finally, the variability in methodologies among the 29 surveys is probably less than that of faunistic surveys of spiders in nonagricultural habitats (see review in Young et al., 1989). We conclude that a hypothetical "high quality" survey would employ several collection methods to sample both foliage- and ground-dwelling spiders, day and night, 12 months of the year, for 3-5 years, and at ten or more locations.

Spider fauna of nine agroecosystems.—Faunal surveys were obtained for nine crop systems in the United States, though not all systems were equally surveyed (Appendix 1). Grain sorghum, guar, and peanuts were surveyed only once, whereas multiple surveys were obtained for rice (2), sugarcane (2), corn (2), alfalfa (4), cotton (7), and soybean (9). Species richness of spiders among the nine crop systems can be grouped into three levels. Cotton contained the most species (≤ 308), with soybean (≤ 262) and alfalfa (≤ 233) in the same high diversity group. Guar (≤ 52), rice (≤ 75), and grain sorghum (≤ 88) comprised the group with the lowest number of species. An intermediate group was represented by peanuts (≤ 131), corn (≤ 136), and sugarcane (≤ 137). The wide disparity in numbers of spider species that occur in these crop systems can be attributed to several factors. Those crops surveyed most frequently had the most species, which suggests sampling bias. A more likely explanation, however, involves the structural complexity of plants. The nine crop plants can be separated into two groups based on growth form: (1) multiple-branching dicotyledonous forms include alfalfa, soybean, cotton, peanuts, and guar; and (2) simple-branching monocotyledonous forms include rice, grain sorghum, sugarcane, and corn. Given the known positive correlation between plant structural complexity and numbers

of associated spiders (Greenstone 1984; Hatley and MacMahon 1980; Uetz 1976), it is not surprising that cotton, for instance, supports many more spider species than rice. Two apparent exceptions to this trend, guar and peanut, may be due to minimal sampling effort.

Considering all field-crop systems as a whole, the spider community is dominated by only a few of the 48 families that occur in all North American habitats. Species of 26 families occur in field crops; 5 families contained 61% of the total field-crop species—Salticidae (89 spp.), Linyphiidae (78), Araneidae (77), Theridiidae (64), Lycosidae (62). Conversely, 6 families were represented by only 1 species. Several genera were represented by large numbers of species in field crops—*Theridion* (19 spp.), *Lycosa* (17), *Xysticus* (16), *Dictyna* (15), *Phidippus* (14). However, of the 192 genera recorded from field crops, 105 were represented by only 1 species (Table 2).

Relation of crop fauna to North American fauna.—Millions of acres annually in North America are occupied by various crop systems. About 22% of the land in the United States is devoted to cropland, with another 8% covered by roads, parking lots, houses, factories, and other structures (Anon. 1987). The remaining 70% is comprised of pastures, rangeland, forests, and margins; these are the sources of spider immigrants to field crops. About 3311 species of spiders in 470 genera and 48 families are found in North America (Roth 1985) (Table 2). Fifty-four percent of the families, 41% of the genera, and 19% of the species also occur in field crops. At least one exhaustive field survey of the spiders of an entire county indicates that these values for North America may be representative of much smaller areas, as 19% of the species collected in Washington Co., Mississippi, also occurred in field crops (Young et al. 1989).

The ten largest families of spiders in North America comprise 84% of the total number of species. Some of these families, however, are poorly represented in field crops (Table 2). Only 7% of the 252 agelenid species are associated with field crops; likewise 9% of the 845 linyphiid species and 11% of the 159 dictynid species occur in field crops. Conversely, several families are well represented in field crops, e.g., 40% of the 192 araneid species, 31% of the 288 salticid species, and 31% of the 128 thomisid species. Several factors may account for these considerable differences between families. The most difficult spiders to identify are the small-sized species of Linyphiidae. Some faunal surveys avoid this problem by assigning linyphiids to one undifferentiated category, i.e., Erigoninae. Thus, many more species of Linyphiidae likely occur in field crops than are recognized or reported, particularly given their strong aerial dispersal characteristics (Greenstone et al. 1987). Conversely, three of the taxonomically better known spider families - Araneidae, Thomisidae, and Salticidae - are well represented in field crops and known to be strong aerial or ground dispersers (Greenstone et al. 1987; Young, unpubl. data).

One might expect a larger percentage of the total North American spider fauna to occur in field crops. That such apparently is not so suggests that a selection process is occurring, where only certain spider characteristics lead to increased likelihood of occurrence in field crops. These characteristics probably are associated with dispersal and subsequent survival in a highly disturbed and sometimes noxious environment.

Prey-capturing guilds.—Functionally, spider families can be categorized on the basis of prey capture method, e.g., web-spinning or wandering species (Table 2).

Table 2.—Proportions of genera and species of North American spiders that occur in field crops.
a = genera and species data from Roth (1985), b = data from Gertsch (1979), Comstock (1940).
Percentages in parentheses.

Araneomorphae Family	Genera			Species			Prey-capture technique ^b
	N. A. ^a	Field crops	(%)	N. A. ^a	Field crops	(%)	
Agelenidae	25	6	(24)	252	17	(6.7)	Web-Sheet
Amaurobiidae	8	1	(12.5)	82	1	(1.2)	Web-Sheet
Anapidae	1	0		1	0		Web-Orb
Anyphaenidae	5	5	(100)	37	13	(35.1)	Wand-Active
Aphantochilidae	1	0		1	0		Wand-Ambush
Araneidae	42	30	(71.4)	192	77	(40.1)	Web-Orb
Caponiidae	2	0		3	0		Wand-Active
Clubionidae	20	11	(55)	193	47	(24.4)	Wand-Active
Ctenidae	3	0		5	0		Wand-Active
Desidae	1	0		1	0		Web-Sheet
Dictynidae	9	3	(33.3)	159	18	(11.3)	Web-Sheet
Diguetidae	1	0		6	0		Web-Matrix
Dinopidae	1	0		1	0		Web-Orb
Dysderidae	3	2	(66.7)	7	2	(28.6)	Wand-Active
Filistatidae	3	1	(33.3)	13	1	(7.6)	Web-Sheet
Gnaphosidae	24	12	(50)	248	38	(15.3)	Wand-Active
Hahniidae	3	1	(33.3)	19	4	(21.1)	Web-Sheet
Hersiliidae	1	0		2	0		Wand-Active
Homalonychidae	1	0		2	0		Wand-Active
Hypochilidae	1	0		4	0		Web-Matrix
Leptonetidae	2	0		34	0		Web-Matrix
Linyphiidae	152	32	(21.1)	845	78	(9.2)	Web-Sheet
Loxoscelidae	1	0		13	0		Web-Sheet
Lycosidae	16	10	(62.5)	234	62	(26.5)	Wand-Active
Mimetidae	2	2	(100)	13	7	(53.8)	Wand-Ambush
Mysmenidae	3	1	(33.3)	6	1	(16.7)	Web-Orb
Nesticidae	3	1	(33.3)	31	1	(3.2)	Web-Matrix
Ochyroceratidae	1	0		1	0		Web-Sheet
Oecobiidae	2	1	(50)	7	2	(28.6)	Web-Sheet
Oonopidae	8	0		24	0		Wand-Active
Oxyopidae	3	3	(100)	20	6	(30)	Wand-Active
Philodromidae	5	5	(100)	95	28	(29.5)	Wand-Active
Pholcidae	10	2	(2)	31	3	(9.7)	Web-Matrix
Pisauridae	4	2	(50)	14	9	(64.3)	Wand-Active
Plectreuridae	2	0		15	0		Wand-Active
Salticidae	45	33	(73.3)	288	89	(30.9)	Wand-Active
Scytodidae	1	0		9	0		Wand-Active
Selenopidae	1	0		5	0		Wand-Ambush
Sparassidae	3	0		8	0		Wand-Ambush
Symphytognathidae	1	0		1	0		Web-Orb
Telemidae	1	0		3	0		Web-Sheet
Tengellidae	1	0		5	0		Web-Sheet
Theridiidae	27	17	(63)	231	64	(27.7)	Web-Matrix
Theridiosomatidae	1	1		2	1		Web-Orb
Thomisidae	10	8	(80)	128	40	(31.3)	Wand-Ambush
Uloboridae	7	2	(28.6)	15	3	(20)	Web-Orb
Zodariidae	2	0		4	0		Wand-Active
Zoridae	1	1	(100)	1	1	(100)	Wand-Ambush
Totals	470	192	(40.9)	3311	614	(18.5)	

Table 3.—Comparison of two prey-capturing guilds, web-spinning and wandering, for North America and for field crops. Each family assigned to a guild based on data from Roth (1985), Kaston (1981), Gertsch (1979), and Comstock (1940). Percentages in parentheses.

	Web-spinning	(%)	Wandering	(%)
N.A. fauna				
Families	25	(52.1)	23	(47.9)
Genera	307	(65.3)	163	(34.7)
Species	1955	(59)	1356	(41)
Field crops				
Families	13	(52)	12	(48)
Genera	98	(51)	94	(49)
Species	271	(44.1)	343	(55.9)

The North American spider fauna is estimated at the species level to be 59% web-spinners and 41% wanderers (Table 3). The spider fauna of field crops, however, is estimated to be 44% web-spinners and 56% wanderers. Such disparity between the North American fauna and the field-crop fauna may be attributable to several factors, which include dispersal (colonization) differences between guilds and survival differences among disturbed (agricultural) habitats.

Dispersal differences between guilds.—Crop fields are assumed to be composed of spider populations that have emigrated from adjacent habitats or are year-round residents (Luczak 1979). Perennial crops such as alfalfa are more likely to have over-wintering populations of spiders than annual crops such as wheat. However, studies in England surprisingly have demonstrated that spider diversity and density on enclosed land freshly plowed and cultivated in the autumn were maintained until early spring as compared to similarly-treated land where spiders were free to emigrate (Duffey 1978). Unfortunately, the ability of spiders to survive autumnal crop harvest and subsequent soil disturbance has not been investigated in the United States. Thus we are left with the assumption that spiders immigrate each year from adjacent habitats into annual field crops, with minimal overwintering in the crop field. Such immigration occurs aerially by floating on silk threads (ballooning), or by silk-thread bridges between plants, or by ambulatory movements on the ground (Gertsch 1979). Most of the spider individuals that undergo aerial movement in field crops are araneids and linyphiids, both families of web-spinners (Greenstone et al. 1987; Dean and Sterling 1985). Wanderers, e.g., Salticidae and Lycosidae, comprised less than 9% of the aeronauts in some investigations (Plagens 1986; Salmon and Horner 1977). Crop fields and adjacent disturbed habitats may generate proportionately more aerial dispersers than other habitats, because species that occupy these "unstable" habitats have greater aeronautic dispersal powers (Greenstone 1982; Meijer 1977).

Survival differences between guilds.—Only those spider species with good dispersal characteristics are likely to appear in a field crop. Their continued presence in the crop, however, is due to other characteristics, such as their ability to avoid predation, tolerate the typically hot and dry environment, adapt to the particular plant structure and spatial pattern, and find food. In general, web-spinners and wanderers exhibit differences in these abilities. Wandering spiders contain few examples of feeding specialists, with most species capable of capturing a wide diversity of prey types and sizes (Nentwig 1986). One of the

most abundant spiders in field crops is a wanderer, *Oxyopes salticus*, which consumes at least 34 species of insects in 21 families and nine orders (Young and Lockley 1985). Web-spinners, however, exhibit considerable specialization on prey types and sizes (Nentwig 1985). This suggests that wandering spiders may be more likely to find suitable food than web-spinners in a field crop.

Habitat characteristics that are particularly important to web-spinners are plant structure and spacing. Increased availability of substrate for web attachment is usually associated with increased spider density (Rypstra 1983). Many of the larger orb-weavers have specific habitat preferences for particular heights above the ground and large distances between plants (Enders 1974). Such conditions may occur in field crops for only short periods of time or not at all. Sheet-web and tangle-web weavers also have substrate requirements that infrequently are available in field crops (Rypstra 1983). The movement through a crop field of farming equipment associated with cultivation and chemical applications no doubt damages a considerable proportion of the resident spider webs, but probably has less effect on the wandering spiders. Factors associated with the degree of food specialization, the structure of the habitat, and the differential impact of disturbance may be sufficient to explain the relatively lower numbers of web-spinning species in field crops.

Characteristics of the most frequently occurring spiders in field crops.—The 29 faunal surveys considered herein represent a geographic range from New York to Florida to California and a plant-structural range from rice to soybean. Several spider species occur over a wide geographic range and in a variety of crops. Forty-two species (Table 4) are widely distributed among the crop systems investigated thus far and probably represent the most abundant species found in field crops. At least 1/3 of the 42 species average less than 4 mm in body length. Such small spiders probably prey on the smaller pests such as thrips, aphids, and immatures of Heteroptera and Lepidoptera. The dispersal of the eight small-sized linyphiid species (Table 4) is more affected by the unpredictability of air currents than is that of the larger species (Greenstone et al. 1987). Their capture in field crops thus may indicate only recent accidental arrival and not necessarily successful predatory activity. The largest guilds in this assemblage of 42 species are the active wanderers (19 species) and the orb-web spiders (9 spp.), which suggests that active wandering may be the most successful hunting strategy employed by spiders in field crops. Three species—*Tetragnatha laboriosa* Hentz, *Oxyopes salticus*, *Phidippus audax* (Hentz)—have been found in all nine crop systems, usually were the most abundant predators in those crops, and are among the most abundant spiders in North America (Kaston 1978). *Tetragnatha laboriosa* is a small orb-weaver that may leave its web to disperse or search for food and is frequently captured in ground pitfall traps (Culin and Yeargan 1983). Other members of the genus *Tetragnatha* actively seek prey away from the web in ways similar to wandering spiders (Horn 1969). *Oxyopes salticus* is an active wanderer more tolerant of hot and dry crop situations than some other common predators of the southeastern United States (Mack et al. 1988), and was the numerically dominant predator in several crop systems (Young and Lockley 1985). *Phidippus audax* is an active wanderer that is large (body length 8-15 mm), hunts on foliage, often is locally abundant, consumes a wide range of prey sizes, and occurs in many habitats (Roach 1987; Young 1989b). These three species—*T. laboriosa*, *O. salticus*, *P. audax*—are prime candidates for population

augmentation by releases of field-captured or lab-reared individuals, or for population enhancement through habitat manipulations of field crops and adjacent plant communities. As an example of their potential importance, *P. audax* and *O. salticus* are key predators of *Heliothis* spp. and the fleahopper *Pseudatomoscelis seriatus* (Reuter) in cotton and adjacent habitats (Dean et al. 1987). By including field counts of these spiders in the TEXCIM cotton insect management model, predictions of pest abundance and subsequent action recommendations have been improved (Hartstack and Sterling 1988).

Prey of common crop-inhabiting spiders.—Prey choices have been documented for several of the abundant species that occur in agroecosystems (Table 4). *Oxyopes salticus* is known to capture the tarnished plant bug, *Lygus lineolaris* (Palisot) (Young and Lockley 1988), the imported fire ant, *Solenopsis invicta* Buren (Nyffeler et al. 1987a), the bollworm, *Heliothis zea* (Boddie) (Whitcomb 1967), and at least 15 other economically important field-crop pests (Young and Lockley 1985). Crop pests consumed by *P. audax*, besides the three just mentioned, include the spotted cucumber beetle, *Diabrotica undecimpunctata howardi* Barber, the three-cornered alfalfa hopper, *Spissistilus festinus* (Say), the boll weevil, *Anthonomus grandis* Boh., and numerous others (Young 1989b). *Pisaurina mira* (Walck.) (Pisauridae) preys on these six crop pests and also consumes the chinch bug, *Blissus* sp., the leafhopper *Chlorotettix* sp., the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), and a variety of other arthropods (Young 1989c). These same crop pests are fed upon by many other common species of wandering spiders, such as *Metaphidippus galathea* (Walck.) (Salticidae), *Misumenops* spp. (Thomisidae), *Peucetia viridans* (Hentz) (Oxyopidae), *Pardosa milvina* (Hentz) (Lycosidae), and *Chiracanthium inclusum* (Hentz) (Clubionidae) (Plagens 1985; Howell and Pienkowski 1971; Whitcomb and Bell 1964). Small web-spinning spiders such as *T. laboriosa* seem to capture only small flies and aphids (Provencher and Coderre 1987; Whitcomb and Bell 1964), and spin a web that is easily destroyed by wind gusts (LeSar and Unzicker 1978). The common large orb-web spider, *Argiope aurantia* Lucas (Araneidae), spins a strong web capable of capturing large pests such as grasshoppers and scarab beetles, but mostly captures aphids and small flies (Nyffeler et al. 1987b). Thus the various web-spinning spiders that do occur in field crops may have little impact on the "medium-sized" crop pests such as plant bugs, boll weevils, and leaf beetles, and on the non-flying pests such as lepidopterous larvae.

Implications for spiders in IPM programs.—Several management strategies could have immediate positive impacts on spider populations in field crops and lead to increased levels of predation on crop pests. For example, reductions in both chemical applications and cultivation frequencies would kill fewer spiders and destroy fewer webs. Deployment of mulches, non-disturbance of weed covers, and strip planting of diverse crops all increase habitat diversity and consequently would support a larger and more diverse spider community. Augmentation of spider populations by placement of egg sacs in a field also may be feasible. If the pest-management strategy involved reduction of pest numbers in adjacent habitats, then perhaps the most efficient means for accomplishing this would be to conserve and enhance spider populations in these adjacent habitats. Reduction of mowing frequency and herbicide usage in crop margins, as well as the enlargement of such areas, may also result in increased spider populations (e.g., Young 1989a). Of course the easiest tactic to implement is non-intervention, with

Table 4.—Size ranges, hunting techniques, and habitats of the 42 most frequently occurring spiders in U. S. agroecosystems. a = data from Kaston 1978, 1981.

Taxon	Length of adult ♀ (mm) ^a	Hunting technique	Habitat & strata ^a	No. crop systems (out of 9)
ANYPHAENIDAE				
<i>Aysha gracilis</i>	6.4-7	Wand-Act	On foliage	6
ARANEIDAE				
<i>Acanthepeira stellata</i>	7-15	Web-Orb	Tall grass, low bushes	8
<i>Argiope aurantia</i>	19-28	Web-Orb	Tall grass, gardens	8
<i>Argiope trifasciata</i>	15-25	Web-Orb	Tall grass, sunny	7
<i>Cyclosa turbinata</i>	4.2-5	Web-Orb	Bushes	7
<i>Gea heptagon</i>	4.5-5.8	Web-Orb	Low grass & forbs	6
<i>Glenognatha foxi</i>	2	Web-Orb	Meadows & wastelands, low	6
<i>Larinia directa</i>	5-12	Web-Orb	Grass, sunny	7
<i>Neoscona arabesca</i>	5-12	Web-Orb	Tall grass, low bushes	7
<i>Tetragnatha laboriosa</i>	6	Web-Orb	Meadows, bushes, long grass	9
CLUBIONIDAE				
<i>Chiracanthium inclusum</i>	4.9-9.7	Wand-Act	On foliage	8
<i>Clubiona abbotii</i>	4-5.4	Wand-Act	On foliage	8
<i>Trachelas deceptus</i>	3.4-4.2	Wand-Act	Under loose tree bark, rolled up leaves	7
LINYPHIIDAE				
<i>Eperigone tridentata</i>	2.3	Web-Sheet	Under dead leaves in woods	6
<i>Erigone autumnalis</i>	1.4-1.7	Web-Sheet	Grass close to ground, under leaves	7
<i>Florinda coccinea</i>	3.5	Web-Sheet	In grass	7
<i>Frontinella pyramitela</i>	3-4	Web-Sheet	Tall grass, bushes in pine woods	6
<i>Grammonota texana</i>	2	Web-Sheet	Low grass & forbs	6
<i>Meioneta micaria</i>	1.9	Web-Sheet	Ground, low forbs	6
<i>Tennesseellum formicum</i>	1.8-2.5	Web-Sheet	In dead leaves on forest floor	8
<i>Walckenaeria spiralis</i>	2.5	Web-Sheet	Under dead leaves in woods	6
LYCOSIDAE				
<i>Lycosa helluo</i>	18-21	Wand-Act	Ground	7
<i>Lycosa rabida</i>	16-21	Wand-Act	Ground	6
<i>Pardosa milvina</i>	5.2-6.2	Wand-Act	Ground, herbs, low bushes	6
<i>Pardosa pauxilla</i>	4-4.5	Wand-Act	Ground	7
<i>Schizocosa avida</i>	10-15	Wand-Act	Ground	8
OXYOPIDAE				
<i>Oxyopes salticus</i>	5.7-6.7	Wand-Act	Low bushes, herbs	9
PHILODROMIDAE				
<i>Tibellus oblongus</i>	7-9	Wand-Act	Tall grass, bushes	6
PISAURIDAE				
<i>Pisaurina mira</i>	12.5-16.5	Wand-Act	Tall grass, bushes	6
SALTICIDAE				
<i>Habronattus coecatus</i>	5.5	Wand-Act	Ground, grass	6
<i>Hentzia palmarum</i>	4.7-6	Wand-Act	Tall grass, bushes & trees	7
<i>Metaphidippus galathea</i>	3.6-5.4	Wand-Act	Tall grass, bushes	8
<i>Metaphidippus protervus</i>	3.7-6.3	Wand-Act	Tall grass, bushes	6
<i>Phidippus audax</i>	8-15	Wand-Act	Tree trunks, under stones, bushes, tall grass, forbs	9

<i>Phidippus clarus</i>	8-10	Wand-Act	Tall grass, bushes	6
<i>Zygoballus rufipes</i>	3-6	Wand-Act	Dead leaves on ground, herbs, grass, low bushes	7
THERIDIIDAE				
<i>Latrodectus mactans</i>	8-10	Web-Ma	Close to ground	7
<i>Theridion murarium</i>	2.8-4	Web-Ma	Trees, bushes, grass, under stones	6
THOMISIDAE				
<i>Misumenoides</i>				
<i>formocipes</i>	5-11	Wand-Amb	Among flowers	6
<i>Misumenops asperatus</i>	4.4-6	Wand-Amb	In grass & foliage	8
<i>Misumenops celer</i>	5-6.7	Wand-Amb	Grassland flowers	8
<i>Misumenops oblongus</i>	4.9-6.2	Wand-Amb	Grass & weeds	8

no inputs of insecticides, biologicals, cultivations, or other manipulations. Non-intervention allows natural enemies such as spiders to develop unimpeded by man and exert natural controls over potential pest populations; such a tactic actually works in many situations (Sterling et al. 1989).

Both theoretical and empirical studies have demonstrated that generalist predators such as spiders can maintain prey populations at low densities (Post and Travis 1979; Kajak 1978). The conservation and enhancement of generalist (polyphagous) predators in field crops recently has been recommended (Luff 1983; Whitcomb 1981). Dean and Sterling (1987), however, point out the possible negative impacts of spiders on other natural enemies of crop pests, and call for detailed ecological studies to determine the roles of spiders in agroecosystems. Nyffeler and Benz (1987), in a world-wide survey of spiders as natural control agents, also point to the need for detailed ecological studies. Our review should provide the basis for further investigations of field-crop spiders associated with U. S. agroecosystems.

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APPENDIX 1

SPIDERS IN NINE AGROECOSYSTEMS OF THE UNITED STATES

For list of information sources, See Appendix 2.

Taxon	Grain sorghum	Rice	Sugar- cane	Corn	Guar	Peanuts	Cotton	Soybean	Alfalfa
AGELENIDAE									
<i>Agelenopsis aperta</i> (Gertsch)			LA						
<i>A. emertoni</i> Chamb. & Ivie			LA				AR	DE	
<i>A. kastoni</i> Chamb. & Ivie								IL	
<i>A. naevia</i> (Walckenaer)			LA				LA,MS		
<i>A. pennsylvanica</i> (C. L. Koch)							AL,AR	DE,KY	KY
<i>A. spatula</i> Chamb. & Ivie						TX			
<i>Agelenopsis</i> sp.	OK			FL,OH				FL,IA,IL	NY,VA
<i>Cicurina arcuata</i> (Keyserling)			LA				AR		
<i>C. pallida</i> Keys.								IL	
<i>C. robusta</i> Simon			LA						
<i>Cicurina</i> sp.							AL	KY	KY
<i>Coras medicinalis</i> (Hentz)			LA						
<i>C. perplexus</i> Muma			LA						
<i>Coras</i> sp.									KY
<i>Cybaeus</i> sp.								KY	
<i>Tegenaria pagana</i> C. L. Koch			LA						
<i>Wadotes hybridus</i> (Emerton)			LA						
AMAUROBIIDAE									
<i>Titanoea</i> sp.									KY
ANYPHAENIDAE									
<i>Anyphaena celer</i> (Hentz)	OK		LA				AL,TX	KY	
<i>A. laticeps</i> Bryant							AR	FL	
<i>A. maculata</i> (Banks)							AR		
<i>A. pectorosa</i> L. Koch		TX						IL	VA
<i>Anyphaena</i> sp.		AR						DE,IA	NY
<i>Ayscha decepta</i> (Banks)			LA					FL	
<i>A. velox</i> (Becker)			LA	FL					
<i>A. gracilis</i> (Hentz)	OK			FL	OK	TX	AL,AR, LA,MS,TX,	DE,FL IL KY	
<i>Ayscha</i> sp.		AR			TX			IL	VA
<i>Oxysoma cubana</i> Banks								IL	
<i>Teudis mordax</i> (O. P.-Cambridge)				FL			TX		
<i>Wilfilla saltabunda</i> (Hentz)			LA	FL			AL,MS,TX	IL	NY,VA
<i>Wilfilla</i> sp.								DE,KY	KY
ARANEIDAE									
<i>Acacesia hamata</i> (Hentz)				FL			AL,AR,TX	FL	VA
<i>Acanthepeira cherokee</i> Levi							TX		
<i>A. stellata</i> (Walck.)	OK	TX	LA		OK,TX	TX	AL,AR, MS,TX	FL,IL, KY,LA, MO,NC	KY,NY,VA
<i>A. venusta</i> (Banks)							AR		
<i>Acanthepeira</i> sp.				FL	TX			DE,NC	
<i>Alpaida calix</i> (Walck.)							AL		
<i>Araneus guttulatus</i> (Walck.)								IL	
<i>A. juniperi</i> (Emerton)								DE	VA
<i>A. marmoreus</i> Clerck									NY
<i>A. miniatus</i> (Walck.)				FL					
<i>A. nordmanni</i> (Thorell)							AL		
<i>A. pegnia</i> (Walck.)				FL					
<i>A. pratensis</i> (Emerton)									NY
<i>A. thaddeus</i> (Hentz)				OH			AR		
<i>A. trifolium</i> (Hentz)									NY,VA
<i>Araneus</i> sp.	OK			FL,OH	TX		TX	DE,FL, IA,KY,NC	KY,NY,VA
<i>Araniella displicata</i> (Hentz)	OK	TX					AL,AR,LA	IL	NY,VA
<i>Araniella</i> sp.					TX				
<i>Argiope aurantia</i> Lucas	OK	AR	LA	FL,OH		TX	AR,TX	DE,IA,IL, KY,LA,NC	VA
<i>A. trifasciata</i> (Forsk.)	OK			FL,OH	TX	TX	AR,TX	FL,IL, KY,NC	KY,NY,VA

Taxon	Grain sorghum	Rice	Sugar- cane	Corn	Guar	Peanuts	Cotton	Soybean	Alfalfa
<i>Wixia</i> sp.							AR		
<i>Zygiella dispar</i> (Kulczynski)							AL		
CLUBIONIDAE									
<i>Agroeca pratensis</i> Emerton							AL		VA
<i>A. trivittata</i> (Keys.)									CA
<i>Agroeca</i> sp.								KY	
<i>Castianeira alteranda</i> Gertsch						TX			
<i>C. amoena</i> (C.L. Koch)						TX			
<i>C. crocata</i> (Hentz)								LA	
<i>C. descripta</i> (Hentz)			LA	OH		TX	AL,AR	IL	
<i>C. floridana</i> (Banks)								FL	
<i>C. gertschi</i> Kaston							AL,TX	FL	
<i>C. longipalpus</i> (Hentz)			LA			TX	AL,AR LA,TX	FL,LA	
<i>C. occidentis</i> Reiskind						TX			
<i>C. variata</i> Gertsch			LA						VA
<i>Castianeira</i> sp.	OK			FL	TX			IA,KY	KY
<i>Chiracanthium inclusum</i> (Hentz)	OK		LA	FL	TX	TX	AL,AR, MS,TX AL	DE,FL, IL,KY,NC IL	VA
<i>C. mildei</i> L. Koch									NY
<i>Chiracanthium</i> sp.									NY
<i>Clubiona abbotii</i> L. Koch	OK	AR	LA	FL		TX	AL,AR,LA	DE,IL, KY,NC	KY,NY,VA
<i>C. catawba</i> Gertsch							AR	DE	VA
<i>C. johnsoni</i> Gertsch		TX					AR		
<i>C. kagani</i> Gertsch							TX		
<i>C. maritima</i> L. Koch			LA				AL		
<i>C. obesa</i> Hentz			LA				AL		NY
<i>C. pikei</i> Gertsch									VA
<i>C. plumbi</i> Gertsch		TX							
<i>C. procteri</i> Gertsch				FL					
<i>C. pygmaea</i> Banks								FL	
<i>C. riparia</i> L. Koch		TX							
<i>C. salitians</i> Emerton							AR	DE	
<i>C. spiralis</i> Emerton									VA
<i>Clubiona</i> sp.		TX		OH				DE,IA, KY,NC	KY
<i>Clubionoides excepta</i> (L. Koch)							AL		
<i>Myrmecotypus lineatus</i> (Emerton)				FL				FL	
<i>Phrurotimpus alarius</i> (Hentz)			LA				AR		
<i>P. borealis</i> (Emerton)			LA			TX			
<i>P. emertoni</i> Gertsch			LA						
<i>P. minutus</i> (Banks)			LA	FL				FL	
<i>Phrurotimpus</i> sp.									KY
<i>Scotinella fraterna</i> (Gertsch)			LA				AR		
<i>S. pallida</i> Banks							AR		
<i>Scotinella</i> sp.				FL				KY	KY
<i>Strotarchus piscatoria</i> (Hentz)							AL	FL	
<i>Syrisca affinis</i> (Banks)						TX	TX		
<i>Trachelas deceptus</i> (Banks)		AR	LA	FL		TX	AR,LA,TX	FL,LA	VA
<i>T. similis</i> F.O.P.-Camb.			LA	FL				LA	LA
<i>T. tranquillus</i> (Hentz)			LA				AL,AR,MS LA,TX	KY	KY,NY
<i>T. volutus</i> Gertsch									
<i>Trachelas</i> sp.								KY,NC	KY
DICTYNIDAE									
<i>Argenna obesa</i> Emerton								IL	NY
<i>Dictyna annexa</i> Gertsch & Mulaik						TX			
<i>D. bellans</i> Chamberlin						TX			
<i>D. bicornis</i> Emerton	OK					TX			
<i>D. bostoniensis</i> Emerton						TX			
<i>D. consulta</i> Gertsch & Ivie						TX			
<i>D. foliacea</i> (Hentz)									NY
<i>D. hentzi</i> Kaston							AR		NY
<i>D. hoyi</i> Chamb. & Ivie									CA
<i>D. iviei</i> Gertsch & Mulaik						TX			
<i>D. longispina</i> Emerton				OH			TX		

Taxon	Grain sorghum	Rice	Sugar- cane	Corn	Guar	Peanuts	Cotton	Soybean	Alfalfa
<i>D. manitoba</i> Ivie									NY
<i>D. reticulata</i> Gertsch & Ivie							CA		CA
<i>D. segregata</i> Gertsch & Mulaik	OK					TX	AR,LA,TX		
<i>D. subblata</i> Hentz			LA			TX		MO	
<i>D. volucris</i> Keys.					TX	TX	AL,AR,TX		NY,VA
<i>Dictyna</i> sp.	OK	AR		FL,OH	TX	TX		FL,KY	KY
<i>Tricholathys hirsutipes</i> (Banks)									CA
DYSDERIDAE									
<i>Ariadna</i> sp.									KY
<i>Dysdera crocata</i> C. L. Koch			LA						
FILISTATIDAE									
<i>Kukulcania hibernalis</i> (Hentz)							AR,TX	LA	
GNAPHOSIDAE									
<i>Cesonia bilineata</i> (Hentz)			LA				AL		
<i>C. sincera</i> Gertsch & Mulaik						TX			
<i>Drassodes auriculoides</i> Barrows							AR		
<i>D. gosiutus</i> Chamberlin							AR,LA		
<i>Drassodes</i> sp.				FL			AL,TX	DE,KY	KY
<i>Drassyllus creolus</i> Chamb. & Gert.	OK						AR		
<i>D. depressus</i> (Emerton)								IL,KY	KY
<i>D. fallens</i> Chamberlin							AR		
<i>D. gynosphes</i> Chamberlin			LA				AR		
<i>D. lepidus</i> (Banks)	OK					TX	AR		
<i>D. notonus</i> Chamberlin						TX	LA,TX		
<i>D. orgilus</i> Chamberlin						TX			
<i>Drassyllus</i> sp.	OK			FL	TX		AL,AR,TX		CA,VA
<i>Gnaphosa fontinalis</i> Keys.						TX			
<i>G. sericata</i> (L. Koch)			LA	FL		TX	AR,TX	IL,KY	
<i>Haplodrassus signifer</i> (C. L. Koch)						TX			
<i>Haplodrassus</i> sp.					TX				
<i>Herpyllus ecclesiasticus</i> Hentz			LA						
<i>Micaria aurata</i> (Hentz)							AL		
<i>M. triangulosa</i> Gertsch						TX			
<i>M. vinnula</i> Gertsch & Davis							AR		
<i>Micaria</i> sp.				FL		TX			CA
<i>Nodocion floridanus</i> (Banks)							TX		
<i>N. rufithoracicus</i> Worley						TX			
<i>Sergiolus capulatus</i> (Walck.)				FL				IL,NC	
<i>S. lowelli</i> Chamb. & Woodbury						TX			
<i>S. minutus</i> (Banks)			LA				AR		
<i>S. ocellatus</i> (Walck.)			LA				TX		
<i>Sergiolus</i> sp.	OK						MS		KY
<i>Synaphosus paludis</i> (Chamb. & Gert.)			LA				TX	LA	
<i>Urozelotes rusticus</i> (L. Koch)			LA						
<i>Zelotes duplex</i> Chamberlin							AR		
<i>Z. gertschi</i> Platnick & Shadab						TX			
<i>Z. hentzi</i> Barrows	OK						AR,LA		
<i>Z. laccus</i> (Barrows)							AR	IL	
<i>Z. pseustes</i> Chamberlin						TX			
<i>Z. subterraneus</i> (C. L. Koch)							AR		
<i>Zelotes</i> sp.	OK							FL,KY	
HAHNIIDAE									
<i>Neoantistea agilis</i> (Keys.)			LA				AR	IL,KY	KY
<i>N. mulaiki</i> Gertsch						TX	TX		VA
<i>N. riparia</i> (Keys.)									
<i>Neoantistea</i> sp.				FL				DE	
LINYPHIIDAE									
<i>Anibontes longipes</i> Chamb. & Ivie				FL					
<i>Bathypantes albiventris</i> (Banks)				OH					VA

Taxon	Grain sorghum	Rice	Sugar- cane	Corn	Guar	Peanuts	Cotton	Soybean	Alfalfa
<i>M. meridionalis</i> Cros. & Bishop							AR		
<i>M. micaria</i> (Emerton)	OK			FL		TX	AR	IL,KY	KY,VA NY
<i>M. nigripes</i> (Simon)								IL,KY	KY,VA NY,VA
<i>M. unimaculata</i> (Banks)									
<i>Meioneta</i> sp.	OK		LA	FL	TX	TX	AL,TX		
<i>Microlinyphia mandibulata</i> (Emer.)									CA,NY,VA KY
<i>M. pusilla</i> (Sundevall)								IL,KY	
<i>Microneta</i> sp.			LA						
<i>Neriene clathrata</i> Sundevall									NY
<i>N. maculata</i> (Emerton)							AL,AR		VA
<i>N. radiata</i> (Walck.)						TX	AR		
<i>Neriene</i> sp.								FL	
<i>Pimosa</i> sp.									KY
<i>Scylaeceus pallidus</i> (Emerton)	OK								
<i>Spirembolus phylax</i> Chamb. & Ivie							CA		CA
<i>Tapinocyba scopulifera</i> (Emerton)								IL	
<i>Tennesseellum formicum</i> (Emerton)	OK		LA	FL	TX	TX	AL,AR	DE,IL, KY	CA,KY,NY
<i>Walckenaeria pallida</i> Emerton							AL		
<i>W. puella</i> Millidge						TX			
<i>W. spiralis</i> (Emerton)	OK		LA			TX	AR	IL,KY	CA,KY,NY, VA
LYCOSIDAE									
<i>Allocosa absoluta</i> (Gertsch)						TX			
<i>A. floridiana</i> (Chamberlin)			LA	FL					
<i>A. funerea</i> (Hentz)			LA				AR,LA	DE,KY	KY,VA CA
<i>A. mokiensis</i> (Gertsch)									
<i>A. sublata</i> (Montgomery)							AR		
<i>Allocosa</i> sp.							TX		
<i>Arctosa littoralis</i> (Hentz)						TX	LA		
<i>Arctosa</i> sp.							CA		NY
<i>Geolycosa riograndae</i> Wallace						TX			
<i>Geolycosa</i> sp.	OK								
<i>Gladicosa gulosa</i> Walck.	OK						AR		
<i>Lycosa acompa</i> (Chamberlin)			LA				AR		
<i>L. ammophila</i> Wallace				FL					
<i>L. annexa</i> Chamb. & Ivie							AR	FL	
<i>L. antelucana</i> Montgomery	OK		LA			TX	AR		
<i>L. aspersa</i> Hentz			LA						
<i>L. baltimoriana</i> (Keys.)	OK								
<i>L. carolinensis</i> Walck.			LA	FL			AR	KY	KY
<i>L. frondicola</i> Emerton								KY	KY
<i>L. georgicola</i> Walck.			LA						
<i>L. helluo</i> Walck.	OK	TX	LA	FL			AR,LA,TX	DE,FL, KY,LA	NY,NY,VA
<i>L. lenta</i> Hentz			LA	FL				FL	
<i>L. modesta</i> (Keys.)									KY
<i>L. punctulata</i> (Hentz)	OK		LA				AL,AR	DE,FL,NC	KY
<i>L. rabida</i> Walck.			LA	FL		TX	AL,AR, LA,TX	DE,FL, KY,NC	KY,VA
<i>L. ripariola</i> Bonnet								KY	KY
<i>L. timuqua</i> Wallace								FL	
<i>Lycosa</i> sp.	OK	AR		OH	TX			DE,KY,NC	CA,KY
<i>Pardosa atlantica</i> Emerton/ <i>P. saxatilis</i> (Hentz)		AR,TX	LA				AL,AR LA,TX	DE,IA,KY	KY,VA
<i>P. delicatula</i> Gert. & Wall.	OK		LA		TX				
<i>P. distincta</i> (Blackwall)		TX					AL,LA,MS	MO,NC	VA
<i>P. littoralis</i> Banks				FL			AL	FL	VA
<i>P. mercurialis</i> Montgomery						TX			
<i>P. milvina</i> (Hentz)		AR,TX	LA	FL			AL,AR, LA,TX	DE,FL, IL,KY, LA,NC	KY,NY,VA
<i>P. modica</i> (Blackwall)									NY
<i>P. moesta</i> Banks			LA						NY

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Taxon	Grain sorghum	Rice	Sugar-cane	Corn	Guar	Peanuts	Cotton	Soybean	Alfalfa
<i>P. keyserlingi</i> Marx				FL		TX	AL	IL	
<i>P. marxi</i> Keys.								IL	
<i>P. minutus</i> Banks						TX			VA
<i>P. pernix</i> Blackwall							MS		
<i>P. placidus</i> Banks									NY
<i>P. pratariae</i> (Schick)						TX	TX		
<i>P. rufus</i> Walck.							AL	DE	NY
<i>P. satullus</i> Keys.							AR		
<i>P. vulgaris</i> (Hentz)							AR,IA		
<i>Philodromus</i> sp.	OK				TX			DE,KY,NC	KY,VA
<i>Thanatus formicinus</i> (Clerck)						TX	AL,LA, TX	IL	VA
<i>T. rubicellus</i> M. Leitas							AR		
<i>T. striatus</i> (C. L. Koch)							AL		
<i>Thanatus</i> sp.	OK			OH				DE	VA
<i>Tibellus duttoni</i> (Hentz)						TX	AR, TX		
<i>T. maritimus</i> (Menge)		TX							
<i>T. oblongus</i> (Walck.)		TX		OH	TX		AL	IA,IL, KY	CA, KY, NY, VA
<i>Tibellus</i> sp.								DE, FL, NC	VA
PHOLCIDAE									
<i>Pholcus phalangioides</i> (Fueselin)			LA						
<i>Psilochorus redemptus</i> Gert. & Mulaik						TX			
<i>Psilochorus</i> sp.							CA		
PISAUROIDAE									
<i>Dolomedes albineus</i> Hentz			LA						
<i>D. scriptus</i> Hentz		TX	LA						
<i>D. tenebrosus</i> Hentz		TX							
<i>D. iriton</i> (Walck.)		AR, TX					AL, AR, LA, TX	FL, MO	
<i>Dolomedes</i> sp.				FL				NC	KY
<i>Pisaurina brevipes</i> (Emerton)								IL	
<i>P. dubia</i> (Hentz)			LA						
<i>P. mira</i> (Walck.)		TX	LA			TX	AL, AR, LA	DE, FL, IL, KY	KY, NY
<i>Pisaurina</i> sp.	OK			FL				DE, KY	
SALTICIDAE									
<i>Admetina tibialis</i> (C. Koch)							TX		
<i>Agassa cyanea</i> (Hentz)								IL	VA
<i>Ballus youngii</i> G. & E. Peckham							AL		
<i>Corythalia canosa</i> (Walck.)			LA	FL					
<i>Eris aurantia</i> (Lucas)							AL, AR, MS	FL, NC	VA
<i>E. miliaris</i> (Hentz)			LA			TX	AL, LA, MS, TX	IL, KY, LA	VA
<i>E. pinea</i> (Kaston)							AL	IL	
<i>Eris</i> sp.					TX			DE, MO	KY
<i>Euophrys</i> sp.									VA
<i>Evarcha hoyi</i> (G. & E. Peckham)									
<i>Habrocestum pulex</i> (Hentz)							AL, LA, MS	MO	VA
<i>Habrocestum</i> sp.								DE	
<i>Habronatus agilis</i> (Banks)						TX	AL, LA		
<i>H. borealis</i> (Banks)		AR	LA				AL, MS		
<i>H. brunneus</i> (G. & E. Peckham)				FL					
<i>H. calcaratus</i> Banks							AL		
<i>H. coecatus</i> (Hentz)	OK		LA			TX	AL, AR, LA, MS, TX	LA, NC	CA, VA
<i>H. decorus</i> (Blackwall)									NY
<i>H. mustaciatus</i> Chamb. & Ivie							AL		CA
<i>H. texanus</i> (Chamberlin)	OK					TX		IL	
<i>H. trimaculatus</i> Bryant				FL					
<i>H. viridipes</i> (Hentz)	OK						AL, LA, MS		
<i>Habronatus</i> sp.							AL	MO	KY

Taxon	Grain sorghum	Rice	Sugar- cane	Corn	Guar	Peanuts	Cotton	Soybean	Alfalfa
<i>Hentzia mitrata</i> (Hentz)			LA				AL,AR, TX DE,FL,NC		
<i>H. palmarum</i> (Hentz)			LA	FL	TX	TX	AL,AR, LA,MS,TX	DE,FL, IL,NC DE,KY,NC	VA
<i>Hentzia</i> sp.	OK								
<i>Lyssomanes viridis</i> (Walck.)				FL			AL,TX		
<i>Maevia inclemens</i> (Walck.)						TX	AL,LA		
<i>Marpissa bina</i> (Hentz)									VA
<i>M. dentoides</i> Barnes				FL					
<i>M. formosa</i> (Banks)		TX					TX		
<i>M. lineata</i> (C. L. Koch)						TX	TX		VA
<i>M. pikei</i> (G. & E. Peckham)						TX	LA		VA
<i>Marpissa</i> sp.							AL		
<i>Metacyrba taeniola</i> (Hentz)							AR		
<i>Metacyrba</i> sp.								DE	KY
<i>Metaphidippus castaneus</i> (Hentz)							AL TX		
<i>M. exiguus</i> (Banks)							AR,LA, MS,TX	FL,IL,KY, LA,MO,NC	NY,VA
<i>M. galathea</i> (Walck.)	OK		LA	FL	TX	TX			
<i>M. insignis</i> (Banks)	OK						AL,AR,TX CA		
<i>M. manni</i> G. & E. Peckham							AL,AR, LA,MS AR,TX	IA,IL	NY,VA
<i>M. protervus</i> (Walck.)		AR	LA	OH					
<i>M. vitis</i> Cockerell		TX							
<i>Metaphidippus</i> sp.	OK							DE,FL,KY, MO,NC DE	
<i>Neon</i> sp.									
<i>Neonella vinnula</i> Gertsch							TX		
<i>Peckhamia americana</i> (G. & E. Peckham)				FL					
<i>P. picata</i> (Hentz)	OK					TX	AR		
<i>Peckhamia</i> sp.								KY	KY
<i>Pellenes limatus</i> G. & E. Peckham						TX			
<i>Phidippus apacheanus</i> Chamb. & Gert.				FL		TX	LA		
<i>P. audax</i> (Hentz)	OK	TX	LA	FL	OK,TX	TX	AL,AR, LA,MS,TX	FL,IL, KY,LA, MO,NC	KY,NY,VA
<i>P. cardinalis</i> (Hentz)					TX	TX	AR,LA,TX		
<i>P. carolinensis</i> G. & E. Peckham							AR		
<i>P. clarus</i> Keys.			LA	FL,OH		TX	AL,AR, LA,MS,TX	FL,LA, MO,NC	VA
<i>P. insignarius</i> C. L. Koch							AL		
<i>P. mystaceus</i> (Hentz)							AR		
<i>P. pius</i> Schick						TX			
<i>P. princeps</i> (G. & E. Peckham)				OH FL			AL		NY
<i>P. pulcherrimus</i> Keys.									
<i>P. purpuratus</i> Keys.							AL,AR	MO	
<i>P. puinami</i> (G. & E. Peckham)				FL					
<i>P. regius</i> , C. L. Koch				FL			AL	FL	
<i>P. texanus</i> Banks						TX	TX		
<i>Phidippus</i> sp.				OH	OK,TX			DE,FL, IA,MO,NC	CA,KY,VA
<i>Phlegra fasciata</i> ((Hahn)							AL		
<i>Platycryptus undatus</i> (DeGeer)							AL,AR, MS,TX AL		
<i>Plexippus paykulli</i> (Audouin)									
<i>Plexippus</i> sp.								MO	
<i>Salticus</i> sp.					TX				
<i>Sarinda hentzi</i> (Banks)			LA				TX		KY
<i>Sassacus papenhoei</i> G. & E. Peckham	OK				TX	TX	TX		
<i>Sitticus cursor</i> Barrows							AL	KY	VA
<i>S. dorsatus</i> (Banks)						TX			

Taxon	Grain sorghum	Rice	Sugar- cane	Corn	Guar	Peanuts	Cotton	Soybean	Alfalfa
<i>S. pubescens</i> (Fabr.)							AL		
<i>Sitticus</i> sp.								DE	KY
<i>Synageles</i> sp.				FL					
<i>Synemosyna formica</i> Hentz			LA				AL,AR		
<i>Talavera minuta</i> (Banks)									NY
<i>Thiodina puerpera</i> (Hentz)	OK	TX				TX	AL,AR,TX	LA	
<i>T. sylvana</i> (Hentz)		TX					AL,MS,TX	FL,MO	
<i>Thiodina</i> sp.				FL				NC	
<i>Tutelina elegans</i> (Hentz)	OK						AL	IL	
<i>T. harti</i> (Emerton)								NY	
<i>Tutelina</i> sp.				OH			AL		
<i>Zygoballus nervosus</i> (G. & E. Peckham)		AR					AR,TX		
<i>Z. rufipes</i> G. & E. Peckham		AR	LA	FL		TX	AL,AR, MS,TX	DE,FL	VA
<i>Z. sexpunctatus</i> (Hentz)		AR					AL,LA,MS	FL,NC	VA
<i>Zygoballus</i> sp.								IA,MO,NC	
THERIDIIDAE									
<i>Achaearanea globosa</i> (Hentz)				FL			AL,AR,TX		
<i>A. tepidariorum</i> (C. L. Koch)							LA	FL	VA
<i>Achaearanea</i> sp.		AR		FL				KY	KY
<i>Anelosimus studiosus</i> (Hentz)				FL			TX		
<i>Argyroides cancellatus</i> (Hentz)							AL		
<i>A. fictitium</i> (Hentz)			LA	FL				KY	
<i>A. trigonum</i> (Hentz)							TX		NY
<i>Argyroides</i> sp.				FL				DE	
<i>Chryso</i> sp.								FL	
<i>Coleosoma acutiventer</i> (Keys.)			LA	FL					
<i>Coleosoma</i> sp.								FL	
<i>Crustulina sticta</i> (O.P.-Camb.)									CA
<i>Dipoena abdita</i> Gertsch & Mulaik			LA						
<i>D. nigra</i> (Emerton)							AR,LA,MS		
<i>Dipoena</i> sp.					TX		AL		KY
<i>Enoplognatha marmorata</i> (Hentz)							AL		
<i>E. ovata</i> (Clerck)									NY
<i>Euryopsis funebris</i> (Hentz)							AL,MS	KY	KY,VA
<i>E. gertschi</i> Levi						TX			VA
<i>E. texana</i> Banks									
<i>Euryopsis</i> sp.								DE	
<i>Latrodectus hesperus</i> Chamb. & Ivie									CA
<i>L. mactans</i> (Fabr.)	OK		LA	FL	TX	TX	AL,AR,CA LA,MS,TX LA	FL,KY, LA,NC	
<i>L. variolus</i> (Walck.)									
<i>Paratheridula perniciosus</i> (Keys.)			LA					FL	
<i>R. fuscus</i> Emerton			LA						
<i>Robertus</i> sp.							AL,MS		
<i>Steatoda albomaculata</i> (DeGeer)							MS		
<i>S. americana</i> (Emerton)								KY	KY
<i>S. erigoniformis</i> (O.P.-Camb.)				FL					
<i>S. fulva</i> (Keys.)						TX			
<i>S. grossa</i> (C. L. Koch)			LA						
<i>S. medialis</i> (Banks)						TX			
<i>S. quadrimaculata</i> (O.P.-Camb.)				FL					
<i>S. transversa</i> (Banks)						TX			
<i>S. triangulosa</i> (Walck.)			LA			TX	AL,TX		
<i>Steatoda</i> sp.					TX				
<i>Theridion alabamense</i> Gert. & Archer			LA						

Taxon	Grain sorghum	Rice	Sugar- cane	Corn	Guar	Peanuts	Cotton	Soybean	Alfalfa
<i>X. californicus</i> Keys.							CA		CA
<i>X. concursus</i> Gertsch						TX			
<i>X. discursans</i> Keys.								KY	KY,NY,VA
<i>X. elegans</i> Keys.							AL, TX	IL	
<i>X. ferox</i> (Hentz)			LA					IL, KY	KY
<i>X. fraternus</i> Banks								IL	
<i>X. funestus</i> Keys.						TX	AR, LA, TX	KY	KY, NY
<i>X. furtivus</i> Gertsch									VA
<i>X. gulosus</i> Keys.						TX	AL	NC	NY
<i>X. lucians</i> (C. L. Koch)									NY
<i>X. pellax</i> O.P.-Camb.						TX			
<i>X. texanus</i> Banks			LA		TX	AR, TX	KY	KY	
<i>X. transversatus</i> (Walck.)							AL		VA
<i>X. triguttatus</i> Keys.							AL	KY, MO	KY, VA
<i>Xysticus</i> sp.	OK	AR		FL, OH	TX		AL, MS	DE, IA, KY, MO, NC	KY, VA
ULOBORIDAE									
<i>Hyptiotes cavatus</i> (Hentz)							AR		
<i>Uloborus glomosus</i> (Walck.)			LA	FL		TX	AL, AR, LA	IL	
<i>Uloborus</i> sp.	OK			FL					
ZORIDAE									
<i>Zora pumila</i> (Hentz)							AL		
Totals = 614 taxonomic entries	88	75	137	136	52	131	308	262	233

APPENDIX 2

Information sources for Appendix 1. Letter and number annotations refer to categories as listed in Table 1.

GRAIN SORGHUM

- OK Bailey, C. L. and H. L. Chada. 1968. Spider populations in grain sorghums. *Ann. Entomol. Soc. America*, 61:567-571.
[A - 1; B - 4; C - 1; D - 1; E - 3,4,5; F - 2.]

RICE

- AR Heiss, J. S. and M. V. Meisch. 1985. Spiders (Araneae) associated with rice in Arkansas with notes on species compositions of populations. *Southw. Natur.*, 30:119-127.
[A - 4; B - 3; C - 1; D - 9; E - 1,6; F - 1.]
- TX Woods, M. W. and R. C. Harrel. 1976. Spider populations of a southeast Texas rice field. *Southw. Natur.*, 21:37-48.
[A - 1; B - 9; C - 1; D - 1; E - 1,3,4; F - 2.]

SUGARCANE

- LA Ali, A. D. and T. E. Reagan. 1985. Spider inhabitants of sugarcane ecosystems in Louisiana: An update. *Proc. Louisiana Acad. Sci.*, 48:18-22.
[A - 3; B - ?; C - 1; D - ?; E - 1,2,3,4; F - 1.]
- LA Negm, A. A., S. D. Hensley and L. R. Roddy. 1969. A list of spiders in sugarcane fields in Louisiana. *Proc. Louisiana Acad. Sci.*, 32:50-52.
[A - 10; B - 6; C - 1,2; D - 8; E - 1,3,4; F - 2.]

CORN

- FL Plagens, M. J. 1985. The corn field spider community: Composition, structure, development and function. Ph.D. Thesis, Univ. Florida, Gainesville. 207 pp.
[A - 3; B - 12; C - 1; D - 6; E - 4; F - 1]
- OH Everly, R. T. 1938. Spiders and insects found associated with sweet corn with notes on the food and habits of some species. I. Arachnida and Coleoptera. *Ohio J. Sci.*, 38:136-148.
[A - 1; B - 3; C - 1; D - 1; E - 4; F - 1.]

GUAR

- OK, Rogers, C. E. and N. V. Horner. 1977. Spiders of guar in Texas and Oklahoma. *Environ. Entomol.*, 6:523-524.
TX
[A - 3; B - ?; C - 1; D - ?; E - 1,3,4; F - 1.]

PEANUTS

- TX Agnew, C. W., D. A. Dean and J. W. Smith, Jr. 1985. Spiders collected from peanuts and non-agricultural habitats in the Texas west cross-timbers. *Southw. Natur.*, 30:1-12.
[A - 3; B - 4; C - 1; D - 3; E - 1,3,4; F - 1.]

COTTON

- AL, Skinner, R. B. 1974. The relative and seasonal abundance of spiders from the herb-shrub stratum of cotton fields and the influence of peripheral habitat on spider populations. M. S. Thesis, Auburn Univ., Alabama. 107 pp.
MS
[A - 4; B - 3; C - 1; D - 27; E - 1,2; F - 2.]
- AR Whitcomb, W. H. and K. Bell. 1964. Predaceous insects, spiders, and mites of Arkansas cotton fields. *Univ. Arkansas Agric. Exp. Stn. Bull.*, 690:1-84.
[A - 6; B - 5; C - 1,2; D - 4+; E - 1,2,3,4,5; F - 2.]
- CA Leigh, T. F. and R. E. Hunter. 1969. Predacious spiders in California cotton. *California Agric.*, 1969:4-5.
[A - 1; B - 12; C - 1,2; D - 3; E - 1,2,3,4,5; F - 2.]
- LA Mysore, J. S. and D. W. Pritchett. 1986. Survey of spiders occurring in cotton fields in Ouachita Parish, Louisiana. *Proc. Louisiana Acad. Sci.*, 49:53-56.
[A - 1; B - 6; C - 1,2; D - 4; E - 1,3,4; F - 1.]

- MS Lockley, T. C., J. W. Smith, W. P. Scott and C. R. Parencia. 1979. Population fluctuations of two groups of spiders from selected cotton fields in Panola and Pontotoc Counties, Mississippi, 1977. *Southw. Entomol.*, 4:20-24.
[A - 1; B - 4; C - 1; D - 30; E - 2; F - 2.]
- TX Dean, D. A., W. L. Sterling and N. V. Horner. 1982. Spiders in eastern Texas cotton fields. *J. Arachnol.*, 10:251-260.
[A - 3; B - 5; C - 1; D - 1+; E - 1,2,3,4; F - 1.]
- TX Kagan, M. 1943. The Araneida found on cotton in central Texas. *Ann. Entomol. Soc. America*, 36:257-258.
[A - 2; B - ?; C - 1; D - 3; E - 4; F - 2.]

SOYBEAN

- DE Culin, J. D., Jr. 1978. Spiders in soybean fields: Community structure, temporal distributions of the dominant species, and colonization of the crop. M. S. Thesis, Univ. of Delaware, Newark.
[A - 1; B - 12; C - 1; D - 7; E - 3,7; F - 2.]
- FL Hasse, W. L. 1971. Predaceous arthropods of Florida soybean fields. M. S. Thesis, Univ. of Florida, Gainesville.
[A - 1; B - 4; C - 1; D - 12; E - 1,3,7; F - 1.]
- FL Neal, T. M. 1974. Predaceous arthropods in the Florida soybean agroecosystem. M. S. Thesis, Univ. of Florida, Gainesville.
[A - 3; B - 4; C - 1; D - 12; E - 1,2,3,4,7; F - 1.]
- IA Bechinski, E. J. and L. P. Pedigo. 1981. Ecology of predaceous arthropods in Iowa soybean agroecosystems. *Environ. Entomol.*, 10:771-778.
[A - 2; B - 4; C - 1; D - 15; E - 1,3,7; F - 2.]
- IL LeSar, C. D. and J. D. Unzicker. 1978. Soybean spiders: Species composition, population densities, and vertical distribution. *Illinois Nat. Hist. Surv. Biol. Notes*, 107:1-14.
[A - 2; B - 4; C - 1; D - 3; E - 1,2,7; F - 2.]
- KY Culin, J. D. and K. V. Yeargan. 1983. Spider fauna of alfalfa and soybean in central Kentucky. *Trans. Kentucky Acad. Sci.*, 44:40-45.
[A - 3; B - 9; C - 1; D - 4; E - 3,7; F - 1.]
- LA Goyer, R. A., D. W. Brown and J. B. Chapin. 1983. Predaceous arthropods found in soybean in Louisiana. *Proc. Louisiana Acad. Sci.*, 46:29-33.
[A - 1; B - 4; C - 1; D - 3; E - 1,3; F - 1.]
- MO Bickensstaff, C. C. and J. L. Huggans. 1962. Soybean insects and related arthropods in Missouri. *Univ. Missouri Agric. Exp. Stn. Res. Bull.*, 803:1-51.
[A - 3; B - 4; C - 1; D - 21; E - 1; F - 2.]
- NC Deitz, L. L., J. W. Van Duyn, J. R. Bradley, Jr., R. L. Rabb, W. M. Brooks and R. E. Stinner. 1976. A guide to the identification and biology of soybean arthropods in North Carolina. *North Carolina Agric. Res. Serv. Tech. Bull.*, 238:1-264.
[A - 4; B - 4; C - 1; D - 40; E - 2,7; F - 1.]

ALFALFA

- CA Yeargan, K. V. and C. D. Dondale. 1974. The spider fauna of alfalfa fields in northern California. *Ann. Entomol. Soc. America*, 67:681-682.
[A - 3; B - 12; C - 1,2; D - 6+; E - 1,2,3,4; F - 1.]
- KY Culin, J. D. and K. V. Yeargan. 1983. Spider fauna of alfalfa and soybean in central Kentucky. *Trans. Kentucky Acad. Sci.*, 44:40-45.
[A - 3; B - 10; C - 1; D - 4; E - 2,3; F - 1.]
- NY Wheeler, A. G., Jr. 1973. Studies on the arthropod fauna of alfalfa V. spiders (Araneida). *Canadian Entomol.*, 105:425-432.
[A - 4; B - 7; C - 1; D - 3; E - 1,3,4; F - 1.]
- VA Howell, J. O. and R. L. Pienkowski. 1971. Spider populations in alfalfa, with notes on spider prey and effect of harvest. *J. Econ. Entomol.*, 64:163-168.
[A - 2; B - 12; C - 1,2; D - 1; E - 1,2; F - 1.]
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Edwards, R. L. and E. H. Edwards. 1990. Observations on the natural history of a New England population of *Sphodros niger* (Araneae, Atypidae). J. Arachnol., 18:29-34.

OBSERVATIONS ON THE NATURAL HISTORY OF A NEW ENGLAND POPULATION OF *SPHODROS NIGER* (ARANEAE, ATYPIDAE)

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ABSTRACT

The surface portion of the tube webs of *Sphodros niger* Hentz lies hidden at the interface between duff and overlying pine needles in early successional pitch pine-oak woods on Cape Cod, Massachusetts. Males search for females in June. Spiderlings hatch in August and leave the mother the following April. Millipedes appear to be the principal food item. The surface tubes of older juvenile spiders vary from 13 to 15 cm in length and tend down slope. The surface tube has the consistency of thin parchment. The underground portion varies little in length, averaging 13 cm, and is a simple cylinder. The only adult female web found had a surface tube 63 cm in length. This female had at least 73 spiderlings.

INTRODUCTION

Since the revision of *Sphodros* by Gertsch and Platnick (1980), at which time 47 specimens of *Sphodros niger* Hentz were examined, the number of *S. niger* specimens taken by various collectors has significantly increased (Beatty 1986; Morrow 1986). Most of these new specimens are males, taken when they were searching for females, usually during the month of June. One male was picked up by Jonathan Coddington during the American Arachnological Society's field trip to Martha's Vineyard in 1987. In this case the specimen was dead, found in the web of a black widow spider. On the same day Vincent Roth and S. Beshers also collected a male at Walden Pond, Mass. Carol Senske, daughter of the senior author, collected a male on her property in Green Lane, Pennsylvania in early June, 1984. Beginning in 1985 we have consistently picked up live males in the Falmouth, Massachusetts area between the dates of 12 to 25 June. The objective of this paper is to report on the results to date of our study of this elusive spider.

RESULTS AND DISCUSSION

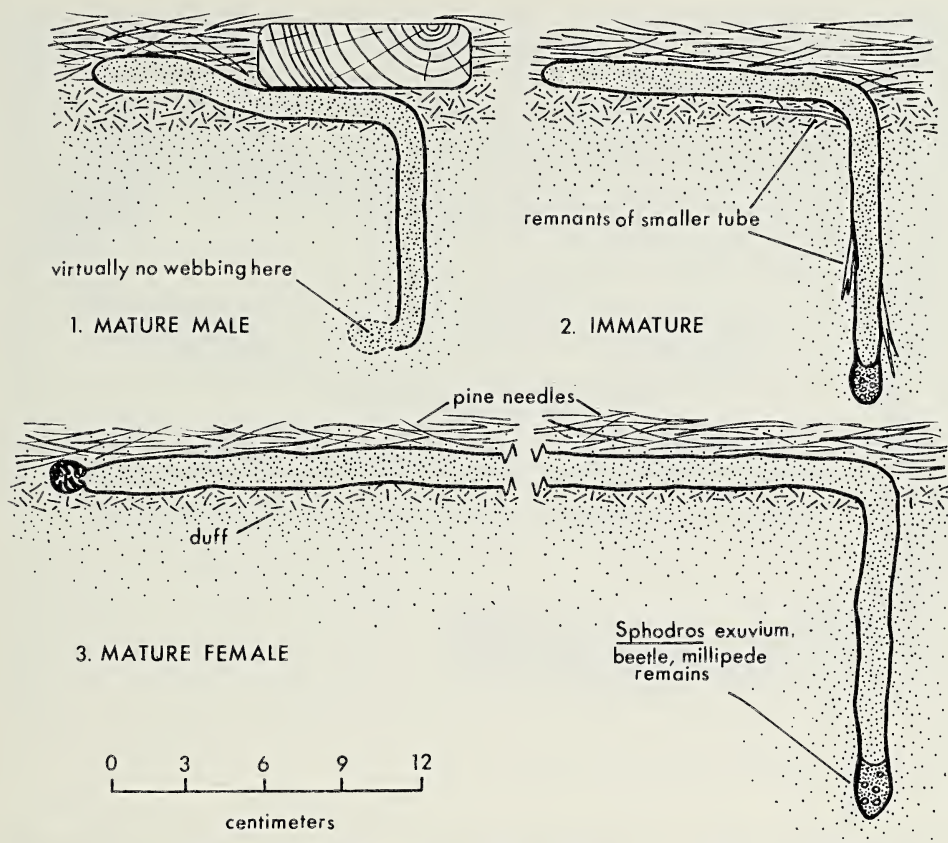
Habitat and web location.—We are aware of two concentrations of the species in the southwestern corner of Cape Cod. Both are found in early successional pitch pine (*Pinus rigida*) habitat with scattered white oaks (*Quercus alba*) and junipers (*Juniperus virginiana*). The understory is variable, with only thinly scattered grass under the pines in one area and a considerable amount of low bush blueberry, scrub oaks, reindeer lichen (*Cladonia* sp.) and grass in the other.

A thorough search of the area for the tube webs followed the first capture of a male in a pitfall trap in 1984. The search was unsuccessful. Further searches were carried out following the observations reported by Beatty, op. cit. The open, grassy areas in the woods were without webs. Almost by accident, a recently vacated web was found in the woods, near where a male had been found (Fig. 1). Efforts were redoubled following this find in and around the barer areas within the woods, in circumstances where the spiders might have portions of their webs under rocks, logs, tree roots, and other objects, again without success. Ultimately we discovered that the preferred situation was one where there was a thick cover of pine needles over duff, in generally bare areas and with the duff thick enough to remain fairly moist through much of the summer. The above-ground capture tubes lie underneath the needles and are therefore completely hidden from view. The soil in this area is a coarse, sandy soil that retains little moisture. To say that this spider is cryptic is an understatement.

Without exception the webs are on the slopes of gently rounded gullies, one to three meters in elevation above the bottom. Webs were considerable distances apart, averaging about 5 m from one another. No concentration such as that described by Beatty (op. cit.) was observed. The majority found were those of larger immature spiders (over 12 mm long). Only one unoccupied tube of a much smaller individual was found, although the remnants of smaller tubes were twice found attached to larger occupied tubes (Fig. 2).

Web architecture.—The webs of these immatures were more or less consistent in their structure and length. In ten of the twelve tubes found so far, the surface portion of the tube paralleled the duff-pine needle interface, averaged 13 cm in length and invariably ran down slope. A relatively sharp, right angle turn led down into the soil for a comparable distance, averaging about 13 cm. The other two webs were found in thickets of low bush blueberries where there were no pine needles but rather a year-round accumulation of leaves with leaf mold underneath. The layout of the webs was otherwise just like those found in the pine needles.

There is no obvious widening of the spider's retreat at the bottom. Usually at the very bottom a centimeter or more of compacted material had accumulated, including *Sphodros* exuvia and a quantity of separated scutes of millipedes. The surface portion of the tube (Fig. 4) has attached material comparable to that found in the duff, while the subterranean section has a thin coating of soil. The attached material is exactly what is external to the tube and may have become attached as the web was constructed, not necessarily as a consequence of any deliberate activity on the part of the spider. In our experience thus far with captive *S. niger*, if the surface portion of the tube is left exposed, the spider makes no attempt to disguise it and will eventually abandon it if left uncovered.



Figures 1-3.—Diagrams of the placement of *Sphodros niger* tube webs and burrows. 1, horizontal portion partially under rotting board; 2, typical web of older juveniles; 3, gap indicates 32 cm of web not shown.

The internal diameter of the horizontal tubes varies from 10 to 12 mm. This is a roomy diameter considering the size of the spider. The inner surface of the horizontal tube is a very light grey in color, smooth and parchment-like in consistency and very strong. If carefully uncovered the tube retains its integrity. The underground portion is soft and flexible, and fairly easily pulled apart. In two cases, the horizontal portion separated from the vertical portion while the pine needle cover was being pulled aside. The horizontal portion of the tube web of an adult female with young, found in August 1988, was unexpectedly long (63 cm; Fig. 3). The vertical portion was exactly like all the others. The end of the horizontal portion of the tube had been collapsed or drawn up by the spider and was compacted into a fairly solid wad.

Behavior of captives.—At the time of this writing (January, 1989) we are keeping several specimens in captivity. It is impossible to make direct observations without disturbing them, since their natural cover has been recreated; consequently we have made only limited behavioral observations. Captive *S. niger* are quick to make new subsurface tubes, but do not reconstruct the surface portion readily. If the subsurface portion of the original tube is placed in a prefabricated hole with the horizontal portion attached and covered with pine needles, the spider will use the entire tube. Those without horizontal tubes

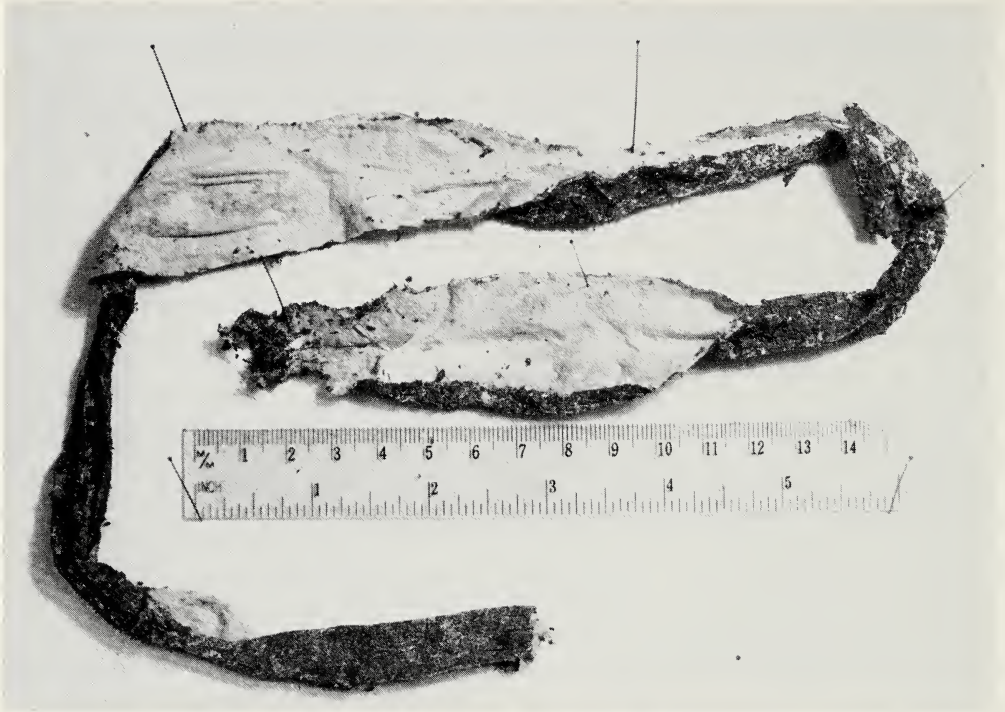


Figure 4.—The surface portion of the web of a mature female *Sphodros niger*, minus a 7-cm piece and the underground section (13.5 cm). See text for details.

usually do a great deal of excavating, and piles of dirt soon appear at the surface around the upper ends of their tubes. This behavior is reminiscent of an observation of Beatty's (op. cit.), in which he observed piles of dirt in and at the end of a tube. At first this activity was puzzling, but eventually we concluded that it usually preceded the construction of a new surface tube originating some distance from the original point of entrance of the old tube into the ground. The spider digs a new exit from below—it does not leave what web it has to start an entirely new tube from the surface.

Webs were not found where the duff and leaf cover were thick enough to encourage mice and shrews (esp. *Blarina brevicauda* and *Sorex cinereus*) to forage and dig burrows. This could be as much a consequence of predation by mammals as choice.

Food and feeding.—These spiders seem to be little disturbed when removed from their habitat if they are left in their tube. One spider almost immediately seized and ate a small caterpillar that wandered across its tube while the web was laid out in the bottom of a plastic pail, barely an hour after it had been removed from its natural surroundings. Another juvenile spider, shortly after being placed in its new home, opened its tube to toss out its shed exuvium.

Judging from the debris found in the bottoms of their tunnels, *S. niger* appears to favor millipedes for food. A few beetle elytra were found as well. It is unlikely that flies, caterpillars or other aerial and surface arthropods would have ready access to the tube. The most abundant insects of any size in the duff-needle interface are various species of carabid beetles, themselves predators. One carabid genus *Pterostichus* sp., quickly caught and devoured a captive *Sphodros* that had

left its web. Another *Pterostichus* was found in an unoccupied web. There are a few spiders, notably *Steatoda americana* (Emerton), *Agelenopsis kastoni* Chamberlin & Ivie, and some lycosids in shallow retreats that occasionally are found in small numbers at the duff-needle interface. Centipedes and sowbugs occur here in fair number while millipedes are usually abundant. Earthworms are infrequently observed in this situation but cannot be ruled out as potential prey.

Spiderlings.—The one female found with young on 14 August 1988, had 73 spiderlings in the horizontal portion of the web and an unknown number below that in the vertical section. The spiderlings were transferred to the vertical portion along with the adult and placed in an aquarium for observation and study. The newly hatched spiderlings are unpigmented except for the eyes, well stocked with yolk, and possess relatively underdeveloped limbs and spinnerets. In terms of general body size and shape, the newly hatched spiderlings are slightly larger than those that leave in the spring. In the wild the young leave the mother in April, at which time they are moderately pigmented light brown in color, have become more slender, look like miniature adults and measure from 2.5 to 2.6 mm. We have yet to observe any ballooning activity on the part of the young—the few captured in the wild were taken in a pitfall trap.

Behavior of males.—In any particular year males move about for approximately a seven day period, but exactly when this activity occurs, is not predictable. In 1984, 1985, and 1986, movement was during the second to third week in June, and in 1987, the fourth. No observations were made in 1988. So far we have detected no obvious climatic events, such as rainstorms, which trigger this activity. On several occasions we followed males during their mating “walkabout” for considerable periods of time. They move rapidly for short distances, usually only several feet, before they take cover and remain quiet for varying periods of time. They tend to move down slope, but the movements otherwise do not seem to be directed. They were most frequently seen in the early afternoon. Attempts to follow males were unsuccessful and frustrating. They were easily lost in vegetation and debris, or occasionally remained stationary for very long periods of time (hours).

Comparisons with other species of *Sphodros*.—There are similarities and differences between the webs and behavior of *S. niger* and those of *abboti* and *rufipes* as noted by Coyle and Shear (1981). The males of *abboti* behave much as *niger* when in search of mates. They are diurnal and seem to rely in part on a contact pheromone which helps to explain our observations of the behavior of *niger* males. In addition *niger* males both move like and have the appearance of pompilid wasps or larger, dark gnaphosids. Our single surface web of an adult female *niger*, 63 cm in length, was about twice as long as the maximum length of the aerial webs of adult female *abboti* and *rufipes* (35 cm). The number of young, 73 plus for our single female *niger* is comparable to the average of 79.7 for six broods of *abboti*. The surface portion of the *niger* web is substantially tougher than the underground portion; the reverse is true of the other two species.

ACKNOWLEDGMENTS

We are grateful to W. A. Shear, F. A. Coyle, and J. A. Coddington for comments and suggestions on the manuscript. H. Guarisco kindly provided some needed literature.

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WATER AND HEMOLYMPH CONTENT IN THE WOLF SPIDER *LYCOSA CERATIOLA* (ARANEAE, LYCOSIDAE)

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ABSTRACT

Female *Lycosa ceratiola*, most of whom were gravid when collected in March in Florida, contained significantly less water than males (2.24 versus 2.88 mg water/mg dry mass, representing 69 and 74% of wet mass, respectively). Both sexes had similar amounts of hemolymph in their bodies (32.4% of wet mass in females and 37.3% in males). The density of hemolymph in male and female spiders at 22-24° C averaged 1.00 mg/ μ l. These results suggest that egg production in female spiders affects their total water content, most likely because ripening eggs gain energy-rich lipids at the expense of water. Two commonly used water content indices, which express water mass as a proportion of either wet or dry body mass, are evaluated.

INTRODUCTION

Water and blood relations in spiders are poorly understood compared to information concerning insects, mites, and ticks. Moreover, the state of the field is heterogeneous: many basic physiological problems in spiders have attracted little attention, whereas a few topics, most notably hemolymph ionic and biological chemistry, have been well investigated (Pulz 1987; Strazny and Perry 1987; and references therein).

Here I attempt to resolve two apparently contradictory concepts underlying variability in water content in spiders (Pulz 1987). The first concept is that there is no consistent difference in water content between the sexes within a species. The second principle is that individual water content depends in part on lipid content, which is high in gravid females compared to males. I hypothesized that water content in gravid females should be significantly less than in males of a given species. Furthermore I hypothesized that the blood content of spiders might also show a similar sexual difference.

I here report on experiments with the wolf spider *Lycosa ceratiola* Gertsch and Wallace that test these ideas. In addition, I discuss the indices used to express water content in spiders. To my knowledge this is only the second study of hemolymph content in a spider. In this study I express water or hemolymph content as the proportion of spider body mass (Allen 1974).

MATERIALS AND METHODS

Adult male and female *L. ceratiola* ($N = 148$) were collected in March in xeric scrubby flatwoods at the Archbold Biological Station, Highlands County, Florida. At this time of year, as indicated by preliminary field surveys, reproduction is prevalent in this species (J. E. Carrel, unpublished observations). Spiders were maintained individually in plastic containers as described by Carrel and Eisner (1984). Their wet mass when alive was measured individually to the nearest 0.1 mg shortly before being used in tests. Individual spiders were used only in one test.

Water content of *L. ceratiola* was determined gravimetrically. Adult spiders ($N =$ eight of each sex) were weighed, placed individually in a tared vial, killed by freezing, and then dried to constant mass in an 80° C oven. Water content was expressed as % wet mass and mg water/mg dry mass.

To calculate hemolymph content (% wet mass) I determined density and volume of hemolymph in spiders. Hemolymph density was measured in spiders ($N =$ eight of each sex) as follows: individuals were anesthetized with carbon dioxide gas; a leg was amputated at the base; discharged hemolymph (2.7-11.1 μ l) was taken up in a volumetrically calibrated tube previously weighed to 1 μ g on a Cahn 28® electrobalance; the filled tube was reweighed and the volume of fluid in it was measured. Density of each hemolymph sample was calculated by dividing its volume by its mass (mg/ μ l).

Hemolymph volume in adults ($N =$ eight of each sex) was determined using the radiolabeled inulin dilution method (Wharton et al. 1965). Injection (5 μ l) was accomplished with a micrometer syringe into the pericardial region of the abdomen of a spider anesthetized with carbon dioxide gas. Carboxy-14C-inulin (sp. act. 2.60 mCi/gram, Sigma Chemical Co.) was dissolved in spider saline (Rathmayer 1965) to achieve a dosage of 0.1 μ Ci per spider. Each spider was again anesthetized 1 h after injection and hemolymph was collected as previously described. The hemolymph was discharged immediately from the tube into 1 ml deionized water in a scintillation vial. Subsequently 15 ml of Aquasol scintillation fluid was added to each vial and radioactivity was measured in a Hewlett-Packard Tri-Carb 460C® scintillation counter. In a similar fashion the radioactivity in aliquots of the inulin stock solution was measured and used as a reference standard. To correct for counting inefficiencies and quenching effects, the sample channel ratio (SCR) was used to calculate total radioactivity (cpm) in each sample. Hemolymph volume of each spider was calculated as follows:

$$V_b = \frac{V_s C_i}{C_s} - V_i$$

where: V_b = volume of hemolymph in spider

V_s = volume of hemolymph sample

V_i = volume of solution injected (5 μ l)

C_i = count of solution injected

C_s = count of hemolymph sample

The reproductive state of female *L. ceratiola* ($N = 100$) was determined in two ways. Using the method of Riddle (1985), 50 spiders were killed by freezing and their abdomens were bisected. Specimens with an egg mass greater than one-sixth of the cross-sectional area of the abdomen were considered gravid. To verify this

Table 1.—Dry mass and water content in adult *Lycosa ceratiola*. Differences between values with the same letter in a column are significant (a = $P < 0.001$; b = $P < 0.01$) with *t*-test. Mean \pm SE, (Range).

Sex	Dry mass mg	Water content		N
		% wet mass	mg water/mg dry mass	
Male	80.1 \pm 8.9 ^a	74.0 \pm 0.9 ^b	2.88 \pm 0.14 ^b	8
	(48.3 - 117.2)	(71.3 - 78.2)	(2.48 - 3.58)	
Female	228.2 \pm 26.4 ^a	69.0 \pm 1.1 ^b	2.24 \pm 0.10 ^b	8
	(157.5 - 388.4)	(61.5 - 71.2)	(1.59 - 2.47)	

procedure, the remaining 50 spiders were inspected at 2-3 day intervals for 4 wk to ascertain whether each had produced an egg sac.

Statistical analyses of the data were performed manually using the methods described in Sokal and Rohlf (1987) or by computer using SAS routines (SAS 1985).

RESULTS AND DISCUSSION

Living adult *L. ceratiola* exhibited a sexual size dimorphism. Data ($\bar{X} \pm$ SE, $N = 24$ of each sex) showed female and male spiders weighed 724 ± 56 and 305 ± 29 mg, respectively. This difference, a factor equal approximately to 2.37, was highly significant (*t*-test, $P < 0.001$). Female spiders are larger than males, presumably because females invest much more in reproduction than males (Gertsch 1979; Foelix 1982). There was no significant difference (ANOVA, $P > 0.01$) in wet body mass among spiders used in different experiments.

Female *L. ceratiola* contained proportionately more dry mass and, therefore, less water than males (Table 1). By either index used in Table 1, water content in female spiders was significantly less than in males. The female/male dry mass ratio was 2.85, approximately 20% higher than the wet mass ratio.

Whole body water content in *L. ceratiola* was slightly less than generally reported for adult spiders from a variety of biomes in North America (Stewart and Martin 1970; Vollmer and MacMahon 1974; Riddle 1985). In all of these studies the spiders were well watered in the laboratory, so dehydration should not be a significant factor. Moreover, Vollmer and MacMahon (1974) found no correlation between habitat aridity, body mass, and interspecific differences in water content of spiders. Surely the relationship between water content and physiological ecology in spiders is sufficiently complex that many more data from many more species are needed to discern life history patterns.

Density and relative amount of hemolymph was similar in male and female *L. ceratiola* (Table 2). Females contained relatively less hemolymph than males, but because of the variability in the data, the difference between the sexes was not significant (*t*-test, $P > 0.05$). Whether the high degree of intrasexual variability in hemolymph content is biologically meaningful or the result of an artifact remains to be determined.

To my knowledge this is the first report of using dilution of radiolabeled inulin injected into spiders. Stewart and Martin (1970), using unlabeled inulin as a blood-born dye, reported the hemolymph in male and female *Dugesia hentsi*

Table 2.—Hemolymph density and content in adult *L. ceratiola*. Differences between values in the same column are not significant ($P > 0.1$) with *t*-test. Mean \pm SE, (Range).

Sex	Hemolymph density mg/ μ l	Hemolymph content % wet mass	N
Male	1.003 \pm 0.007 (0.97 - 1.03)	37.3 \pm 2.4 (28.2 - 46.9)	8
Female	1.000 \pm 0.005 (0.98 - 1.02)	32.4 \pm 6.5 (26.6 - 41.6)	8

averages 19.65 and 18.10%, respectively, of wet body mass. Although the hemolymph content in *D. hentzi* adults is about one-half as much as in *L. ceratiola*, a difference which in part could result from using different methodologies, nevertheless within each species females tend to have less hemolymph than males.

A majority (74%) of 50 female *L. ceratiola* examined internally were found to be gravid. This method was verified by the finding that a smaller, but insignificantly different percentage (58%) of 50 females actually produced egg sacs when maintained for 4 wk in the laboratory (chi-square test, $P > 0.05$). Hence, lipid content of female spiders used in these water and blood content studies presumably was high because most of them contained energy rich eggs. The energy density of spider eggs, expressed as joules/g dry mass, generally is 11% higher than the average for nongravid adult spiders (Anderson 1978).

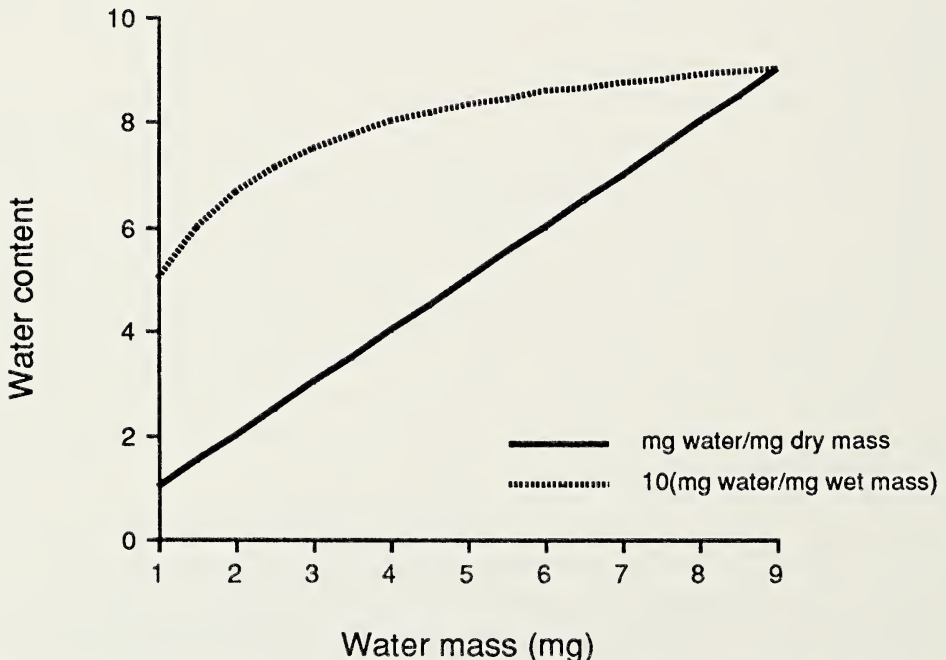


Figure 1.—Comparison of two indices for water content in a hypothetical spider having dry mass of 1 mg as a function of its absolute water mass. (See text for details). The range of water content values matches those actually found in various spiders under different conditions, as summarized by Pulz (1987). For graphical purposes, water content based on wet body mass is shown at one-tenth scale so that the two lines are similar in scope.

As indicated in Table 1, the water content of whole spiders can be expressed by two different indices, one based on the wet mass and the other based on the dry mass of the animal. Most authors, as cited by Pulz (1987), have used the wet mass index, often referred to as "percent water". But is one index scientifically more robust than the other? One way to answer this question is to examine how body water content changes as a function of water mass in a spider, under idealized conditions where dry mass is kept constant (say equal to 1 mg) as if the animal is undergoing dehydration or rehydration. As shown in Fig. 1, under these hypothetical conditions the two indices yield two rather different graphs: the wet mass index levels off asymptotically as the spider gains a lot of water, whereas the dry mass index rises in a linear fashion across the same range.

From this graphical analysis, clearly the linear dry mass index is preferable to the curvilinear wet mass index of body water content. An example will illustrate this conclusion. At high moisture levels, a one percent gain or loss in water content based on a spider's wet body mass translates into a large change approximating 1 mg water/mg dry mass of the animal.

In conclusion, this study shows that a consistent difference in water content between the sexes of *L. ceratiola* can be found when females are gravid. The presence of eggs evidently increases the lipid and dry mass contents in female spiders, causing a slight (5%) decline in water content in comparison to male spiders.

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KARYOTYPES OF SEVENTEEN USA SPIDER SPECIES (ARANEAE, ARANEIDAE, GNAPHOSIDAE, LOXOSCELIDAE, LYCOSIDAE, OXYOPIDAE, PHILODROMIDAE, SALTICIDAE AND THERIDIIDAE)

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ABSTRACT

Karyotypes are reported for 17 species from eight families of spiders from Texas and Missouri. Chromosomal counts (2N) are as follows: Araneidae—*Eustala emertoni*, 24; Gnaphosidae—*Cesonia sincera*, 22 and 24; *Nodocion floridanus*, 24; Loxoscelidae—*Loxosceles reclusa*, 18 and 20; Lycosidae—*Lycosa rabida*, 28 and 30; Oxyopidae—*Oxyopes scalaris*, 21; Philodromidae—*Tibellus duttoni*, 29; Salticidae—*Maevia inclemens*, 27 and 28; *Marpissa pikei*, 28; *Metaphidippus galathea*, 27 and 28; *Peckhamia americana*, 22 and 24; *Phidippus audax*, 28 and 30; *Phidippus texanus*, 28 and 30; *Platycryptus undatus*, 28 and 30; *Salicrus austinesis*, 28 and 30; *Tutelina elegans*, 27 and 28; and Theridiidae—*Steatoda triangulosa*, 22 and 24.

INTRODUCTION

A thorough search of the literature indicates chromosomal data (counts) are available for approximately 300 of the more than 30,000 spider species (Gowan 1985; Datta and Chatterjee 1988). Most of these are reported from the Old World and many are identified only at the generic level. This study adds karyotypic data for 14 additional identified species and three that have been previously reported.

MATERIALS AND METHODS

Specimens for the present study were collected from north-central Texas with the exception of *Oxyopes scalaris* Hentz and *Tutelina elegans* (Hentz) which were from eastern Missouri.

The meiotic studies were accomplished by examining the ovaries and testes of penultimate and mature spiders. The meiotic procedure used was an air-dry method developed by Cokendolpher and Brown (1985). The only modification was the stain. The commercially available Diff-Quick Solution II was used to stain the chromosomes. This staining solution consisted of 1.25 g/l thiazine dye mixture, 100% PDC (0.625 g/l azure A and 0.625 g/l methylene blue) and buffer.

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Five-day-old eggs (embryos) were used for the mitotic studies. The procedure followed was a modification of Matsumoto's (1977) method. Substitutions included the use of methanol instead of ethyl alcohol in the fixative, the use of four eggs instead of one, and a pH of 7.0 for the saline solution instead of 7.2. All mitotic preparations were flame dried and stained with Giemsa. The stain was prepared by mixing 2 to 3 ml of Giemsa with 50 ml phosphate buffer (0.469 g sodium dihydrogen phosphate, 0.937 g sodium monohydrogen phosphate/l water).

Chromosome numbers were determined by counting spreads for each species. The most frequent chromosome counts were regarded as the valid number. In mitotic studies, species where two different consistent counts were noted, they were assumed to be due to the sex determining mechanism.

Specimens sacrificed for meiotic studies and females that produced the eggs for the mitotic studies are deposited in the Invertebrate Collection at Midwestern State University.

RESULTS AND DISCUSSION

Eggs are excellent sources of somatic cells that provide good mitotic spreads. At present, spider karyotyping techniques for somatic cells are not sufficient to observe the sex-determining mechanisms. We agree with Matsumoto's (1977) deductions that meiotic preparations are necessary for determination of the sexing mechanisms.

Tables 1 and 2 list the results of meiotic and mitotic works, respectively. The tables indicate the species studied, diploid ($2n$) numbers, sex-determining mechanisms in meiotic studies, and geographic location. References are made to previous studies where researchers examined the same or closely related species. Some counts in this study do not agree with the previously reported results (see Table 1). This may be due to counting error, improper identification or even geographic variation. Representative photographs of all species examined are shown in Figs. 1-25 with the exception of *Lycosa rabida* Walckenaer and *Peckhamia americana* (Peckham and Peckham) which were unavailable.

Datta and Chatterjee (1988) report that 55 species of Araneidae have been karyotyped. The $2n$ number ranges from 14 to 46 with 24 being the most common. Our study is the first to report a karyotype for *Eustala emertoni* (Banks) (Fig. 1). It is $2n=24$, as are 81% of the other Araneidae. Since this is a mitotic study no sex-determining mechanism is confirmed.

According to the literature 13 different species of Gnaphosidae have been reported (Painter 1914; Hackman 1948; Suzuki 1952; Mittal 1961). With the exception of *Scotophaeus blackwallii* (Thorell), which Mittal (1961) reported as having 11 autosomal pairs and an XXO-XXXX sex-determining mechanism, all other Gnaphosidae cytogenetically known have 10 autosomal pairs and an XXO-XXXX sex-determining mechanism (Painter 1914; Hackman 1948; Suzuki 1952; Mittal 1961). *Cesonia sincera* Gertsch and Mulaik (Figs. 2-3) and *Nodocion floridanus* (Banks) (Fig. 4) mitotic studies show this same consistency. These two karyotypes are the first reported for their respective genera.

Our figures show *Loxosceles reclusa* Gertsch and Mulaik (Loxoscelidae) males as $2n=22$ and females as $2n=24$ and a sex determining mechanism of XXO-

Table 1.—Meiotic Studies. Species, diploid number, number of individuals examined (), sex-determining mechanism, geographic location and selected supportive references.

Species	Diploid number		Sex determining mechanism		Geographic location	References
	Male	Female	Male	Female		
ARANEIDAE						
<i>Eustala</i> sp.	24	—	XXO	—	Asia	Mittal 1961
LOXOSCELIDAE						
<i>Loxosceles reclusa</i> Gertsch & Mulaik	18(9)	20(2)		XXO-XXXX	N.A. (TX)	Current study
<i>L. rufipes</i> (Lucas) [prob. <i>L. laeta</i> -see text]	20			XXO-XXXX	S.A.	Diaz & Saez 1966
LYCOSIDAE						
<i>Lycosa rabida</i> Walck.	28(1)	30(1)		XXO-XXXX	N.A. (TX)	Current study
<i>L. rabida</i>	28	30		XXO-XXXX	N.A. (MS)	Wise 1983
OXYOPIDAE						
<i>Oxyopes seratus</i> (L. Koch)	21	22		XO-XX	Asia (Japan)	Suzuki 1952
PHILODROMIDAE						
<i>Tibellus oblongus</i> (Walck.)	24	26		XXO-XXXX	Asia	Sokolov 1962
<i>T. tenellus</i> (L. Koch)	28	30		XXO-XXXX	Asia (Japan)	Suzuki 1952
SALTICIDAE						
<i>Maevia inclemen</i> [reported as <i>M. vittata</i> Hentz]	28	30		XXO-XXXX	N.A.	Painter 1914
<i>Peckhamia americana</i> (Peck. & Peck.)	22(3)	24(3)		XXO-XXXX	N.A. (TX)	Current study
<i>Phidippus audax</i> (Hentz)	28(1)	30(1)		XXO-XXXX	N.A. (TX)	Current study
<i>Phidippus audax</i> (Hentz)	22	24		XXO-XXXX	N.A. (TX)	Pinter & Walters 1971
<i>Salticus austinensis</i> Gertsch	28(7)	30(3)		XXO-XXXX	N.A. (TX)	Current study
<i>S. cingulatus</i> (Panzer)	28	30		XXO-XXXX	Asia	Sokolov 1960
THERIDIIDAE						
<i>Steatoda triangulosa</i> (Walck.)	22(3)	24(5)		XXO-XXXX	N.A. (TX)	Current study
<i>S. bipunctata</i> (L.)	22	24		XXO-XXXX	Europe	Hackman 1948

XXXX (Figs. 5-6). Of the two *Loxosceles* species previously reported, the sex-determining mechanism is identical but they have a different number of autosomal pairs. *Loxosceles rufescens* (Dufour) and *L. rufipes* (Lucas) are reported by Beçak and Beçak (1960) and Diaz and Saez (1966) respectively as $2n=20$. These workers examined only males. Based upon Gertsch's (1967) revision

Table 2.—Mitotic Studies. Species, diploid number, number spreads examined () and geographical location.

Species	Diploid numbers		Geographic location
ARANEIDAE			
<i>Eustala emertoni</i> (Banks)	24(4)		N.A.,(TX)
GNAPHOSIDAE			
<i>Cesonia sincera</i> Gertsch & Mulaik	22(1)	24(1)	N.A.,(TX)
<i>Nodocion floridanus</i> (Banks)	24(4)		N.A.,(TX)
OXYOPIDAE			
<i>Oxyopes scalaris</i> Hentz	21(4)		N.A.,(MO)
PHILODROMIDAE			
<i>Tibellus duttoni</i> (Hentz)	29(3)		N.A.,(TX)
SALTICIDAE			
<i>Maevia inclemens</i> (Walckenaer)	27(4)	28(4)	N.A.,(TX)
<i>Marpissa pikei</i> (Peckham & Peckham)	28(8)		N.A.,(TX)
<i>Metaphidippus galathea</i> (Walckenaer)	27(8)	28(3)	N.A.,(TX)
<i>Phidippus audax</i> (Hentz)	28(39)	30(12)	N.A.,(TX)
<i>Phidippus texanus</i> Banks	28(3)	30(8)	N.A.,(TX)
<i>Platycryptus undatus</i> (De Geer)	28(3)	30(8)	N.A.,(TX)
<i>Salticus austinensis</i> Gertsch	28(1)	30(1)	N.A. (TX)
<i>Tutelina elegans</i> (Hentz)	27(9)	28(8)	N.A. (MO)
THERIDIIDAE			
<i>Steatoda triangulosa</i> (Walckenaer)	22(19)	24(1)	N.A.,(TX)

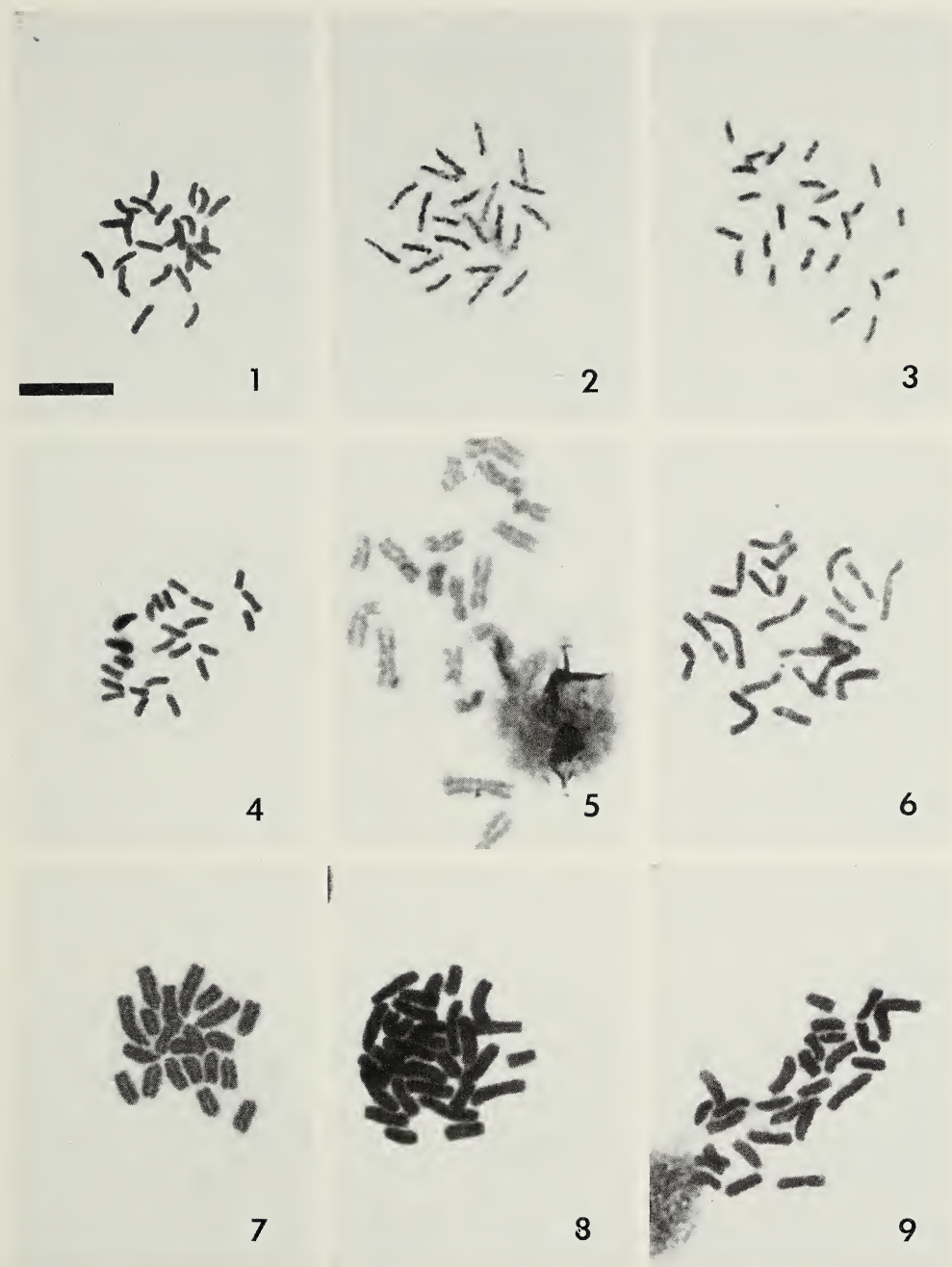
these reported species, *L. rufescens* and *L. rufipes* are probably misidentified and should be *L. gaucho* and *L. laeta* respectively.

Gowan's (1985) survey of the literature revealed karyotypes of approximately 62 different, identified, species of Lycosidae. Diploid counts range from 22 to 30 with 13 autosomal pairs and an XXO-XXXX sex-determining mechanism being the most common. Our findings for *Lycosa rabida* Walckenaer agree with those of Wise (1983) and match the modal number for the family.

In the Oxyopidae three genera and approximately eight, identified, species have been karyotyped (Painter 1914; Hackman 1948; Bole-Gowda 1950; Suzuki 1950, 1952; Sharma and Tandon 1957; Mittal 1961). All but *Oxyopes saliciscus* L. Koch (Painter 1914) and *Peucetia viridana* Stoliczka (Bole-Gowda 1950) have 10 autosomal pairs and an XO-XX sex-determining mechanism. This study revealed that the mitotic spreads of *Oxyopes scalaris* (Fig. 7) had a 2n count of 21.

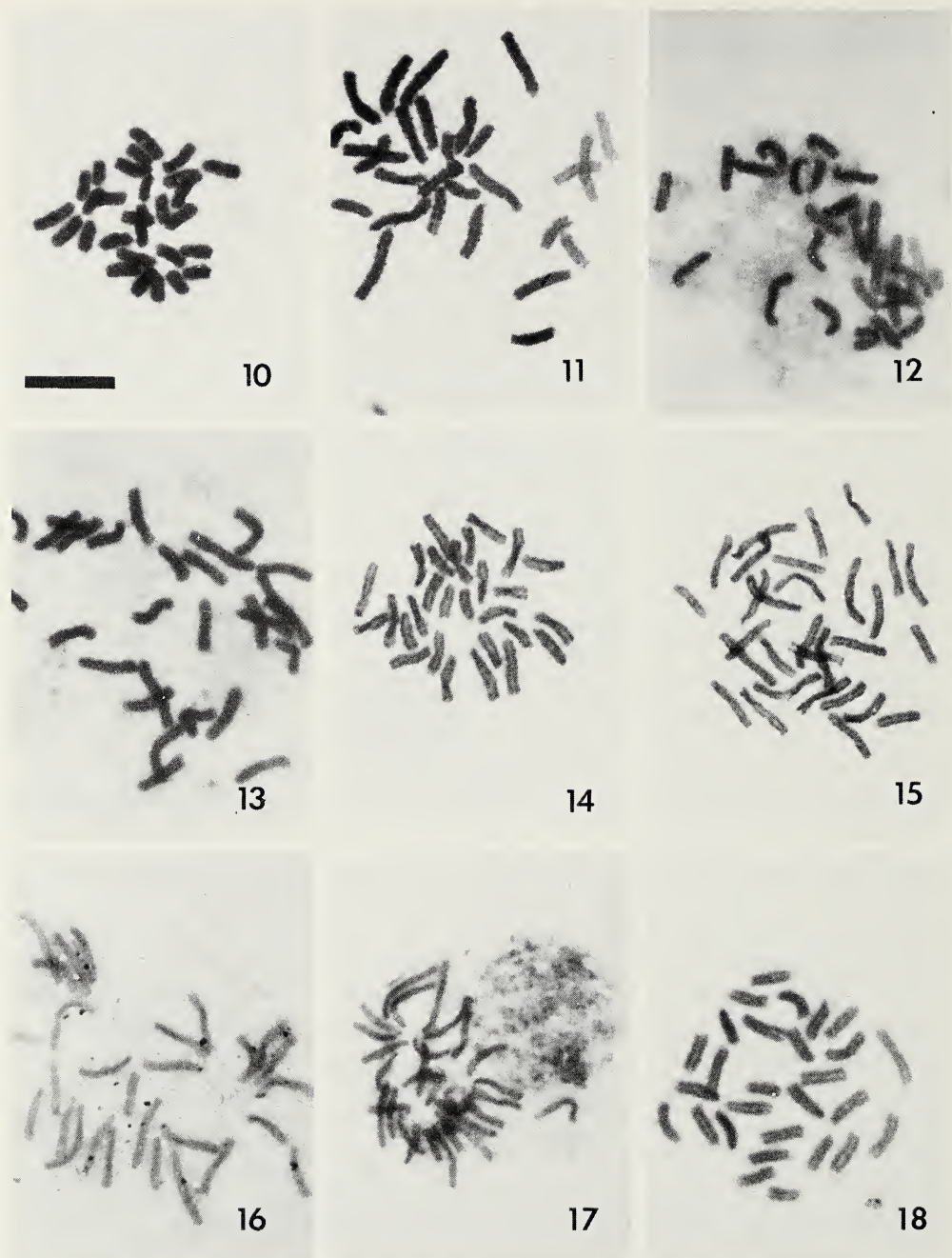
Thirteen autosomal pairs and an XXO-XXXX sex-determining mechanism is the most common number for members of the Philodromidae (Hackman 1948; Sokolov 1960; Suzuki 1952). The 2n count obtained from mitotic spreads for *Tibellus duttoni* (Hentz) (Fig. 8) is 29. Variation from this count has been reported for *T. oblongus* (Walckenaer) (Hackman 1948) and *T. tenellus* (L. Koch) (Suzuki 1952) as indicated in Table 1. Further studies are needed for conclusive counts within the genus and of this species.

Karyotypes from approximately 50 species of Salticidae have been previously reported by Gowan (1985). *Maevia inclemens* (Walckenaer) (Figs. 9-10), previously known as *Maevia vittata* Hentz, was karyotyped by Painter (1914). He worked with two morphologically different males but reported no variation in the chromosome numbers. Only one of the diploid numbers obtained in this study agreed with Painter.



Figures 1-9.—Chromosome spreads of: 1, *Eustala emertoni* $2n=24$; 2,3, *Cesonia sincera*; 2, $2n=22$; 3, $2n=24$; 4, *Nodocion floridanus* $2n=24$; 5,6, *Loxosceles reclusa*; 5, male $2n=18$; 6, female $2n=20$; 7, *Oxyopes scalaris* $2n=21$; 8, *Tibellus duttoni* $2n=29$; 9, *Maevia inclemens* $2n=27$. Scale bar=10 μm .

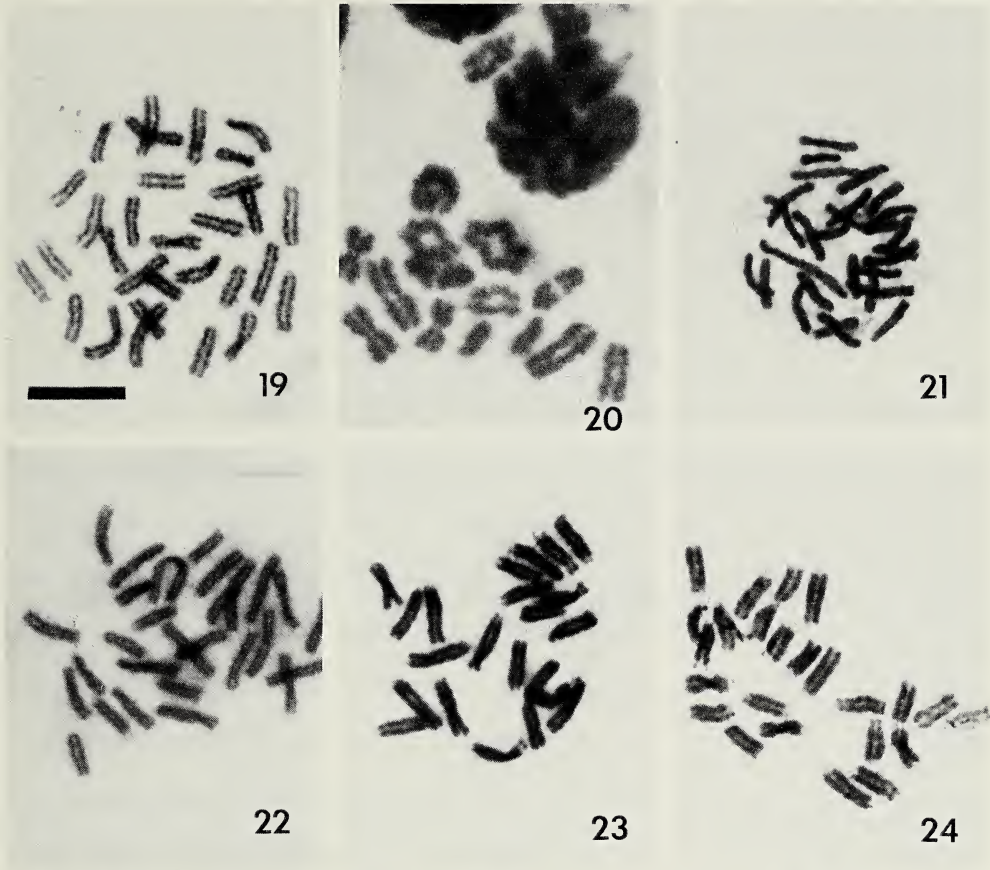
Karyotypes of *Marpissa pikei* (Peckham and Peckham) (Fig. 11), *Metaphidippus galathea* (Walckenaer) (Figs. 12-13), *Peckhamia americana* (Peckham and Peckham), *Platycryptus undatus* (De Geer) (Figs. 18-19) and *Tutelina elegans* (Hentz) (Figs. 21-22) are reported for the first time. As these are



Figures 10-18.—Chromosome spreads of: 10, *Maevia inclemens* $2n=28$; 11, *Marpissa pikei* $2n=28$; 12,13, *Metaphidippus galathea*; 12, $2n=27$; 13, $2n=28$; 14,15, *Phidippus audax*; 14, males $2n=28$; 15, females $2n=30$; 16,17, *Phidippus texanus*; 16, $2n=28$; 17, $2n=30$; 18, *Platycryptus undatus* $2n=28$. Scale bar= $10\ \mu\text{m}$.

also the first reported for each genus no data on related forms are available for comparison.

Phidippus audax (Hentz) (Figs. 14-15) counts do not agree with those reported by Pinter and Walters (1971). However, the meiotic and mitotic counts in this



Figures 19-24.—Chromosome spreads of: 19, *Platycryptus undatus* $2n=30$; 20, *Salticus austinesis* male $n=13$ and XXO (the X's are indicated with arrows); 21,22, *Tutelina elegans*; 21, $2n=27$; 22, $2n=28$; 23,24, *Steatoda triangulosa*; 23, males $2n=22$; 24, females $2n=24$. Scale bar= $10\ \mu\text{m}$.

research were consistent and supportive for $2n$ counts of 28 and 30 with a sexing mechanism of XXO-XXXX. These diploid numbers were also found by Maddison (Gowan 1985). *Phidippus texanus* Banks (Figs. 16-17) diploid counts from mitotic studies were consistent with those of *P. audax*. *Salticus austinesis* Gertsch (Fig. 20) diploid counts agree with *Salticus cingulatus* (Panzer) (Sokolov 1960) and *Salticus scenicus* (Clerck) (Hackman 1948). *Phidippus texanus* Banks and *Salticus austinesis* Gertsch are reported for the first time.

Eight genera and 13 species of Theridiidae have been karyotyped. With the exception of *Chrysso venusta* (Yaginuma) which has 11 autosomal pairs and an XXO-XXXX sex-determining mechanism (Kageyama and Seto 1979) all reported theridiids have 10 autosomal pairs and a XXO-XXXX sex-determining mechanism. *Steatoda triangulosa* (Walckenaer) (Figs. 23-24) typifies this pattern.

Many additional species must be karyotyped, and correct identification determined before assessing any inter- and intra-specific chromosomal variation. With the development of consistent banding techniques in spiders, it may be possible to determine homologies and devise a standard numbering system at least within some genera. It could then be possible to determine the diploid number for each sex from somatic cells such as eggs (embryos).

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EL COMPORTAMIENTO AGONISTICO DE HEMBRAS ADULTAS DE *LYCOSA TARENTULA FASCIIVENTRIS* (ARANEAE, LYCOSIDAE)

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ABSTRACT

Dyadic interactions between adult females of *Lycosa tarentula fasciiventris* in the laboratory are described. Our results show motor patterns that are not very specific to the context, little ritualized fighting, resulting in a high frequency of cannibalism and a great variability in the duration of the sequences.

RESUMEN

Se describen las interacciones diádicas entre hembras adultas de *Lycosa tarentula fasciiventris* en el laboratorio. Nuestros resultados muestran la existencia de patrones motores poco exclusivos del contexto y bajo nivel de ritualización en la lucha, que se refleja en un índice de canibalismo elevado, así como una gran variabilidad en la duración de las secuencias.

INTRODUCCION

El estudio del comportamiento agonístico en las arañas, y en general en todas las especies animales, se ha centrado, fundamentalmente, en las interacciones entre machos adultos (Dijkstra 1969, 1978; Aspey 1976, 1977; Jackson 1982; Halliday 1986). El interés por estos sujetos para tales estudios ha derivado de la función que se adjudica al comportamiento agonístico como técnica de competición intraespecífica por recursos limitados (Wilson 1975).

En el caso de las arañas las hembras presentan, en general, un repertorio comportamental menos complejo que el de los machos no mostrando, por ejemplo, un cortejo activo. Son los machos los que realizan la búsqueda de las hembras, exhibiendo en este contexto una mayor frecuencia de encuentros agonísticos entre ellos, en los que las hembras han sido comúnmente consideradas el recurso por el que compiten (Vollrath 1980; Jackson 1982). Por esta razón se han planteado, con relativa frecuencia, estudios sobre competición, relaciones jerárquicas o relaciones territoriales entre machos adultos (Aspey 1977; Dijkstra 1978; Goist 1982; Austad 1983). Con menor frecuencia, estas mismas cuestiones han sido planteadas con respecto a las hembras adultas (Riechert 1978, 1986; Nosssek & Rovner 1984; Hodge 1987). Sin embargo éstas podrían ser, en algunos casos, los sujetos idóneos para el análisis de estos problemas.

En muchas especies de Lycósidos, los machos no se alimentan tras alcanzar la madurez sexual, pierden la vinculación con un área concreta y vagan en busca de hembras adultas. En *Lycosa tarentula fasciiventris* Dufour, las hembras, por el contrario, suelen permanecer en el nido, donde se alimentan y aparean. Si se admite que el comportamiento agonístico es una técnica de competición por recursos limitados, las hembras podrían ser un buen modelo para su estudio en esta especie, siendo el recurso la ocupación de un nido o de una localización privilegiada para la obtención de alimento (Riechert 1978, 1982).

Nos hemos propuesto analizar el comportamiento exhibido por hembras adultas de *L. tarentula fasciiventris* en interacciones diádicas compitiendo por un nido. En este trabajo presentamos una descripción de la forma en que se desarrolla este comportamiento en dicho contexto, su resultado y sus consecuencias.

MATERIAL Y METODOS

Se han utilizado 40 hembras adultas, recogidas del campo como formas inmaduras, en su antepenúltima fase de desarrollo, en las primaveras de 1984 y 1986. Todos los ejemplares procedían de la zona que rodea a la Universidad Autónoma de Madrid. Desde su captura, fueron mantenidas en el laboratorio en condiciones de humedad, temperatura y alimentación constantes, con iluminación artificial y fotoperiodo de 10 horas de luz y 14 de oscuridad, hasta su observación durante los meses de marzo, abril y mayo de 1985 y 1987, respectivamente. Durante este periodo, permanecieron en terrarios individuales con aislamiento visual del exterior, realizándose registros periódicos del peso y de la respuesta a las presas, así como medidas del tamaño corporal en cada una de las mudas que sufrieron los animales. Al alcanzar la fase adulta, los individuos fueron medidos; se utilizó como criterio de su tamaño el producto de la longitud por la anchura del prosoma (Aspey 1977).

Las observaciones se realizaron en terrarios de 30x15x15 cm, con paredes lisas y opacas y sustrato de tierra. El nido se construyó artificialmente adosado a la pared anterior, de forma que su interior pudiera ser visible durante los periodos de observación; fuera de estos periodos, permaneció aislado visualmente del exterior.

Las arañas se observaron por parejas formadas al azar en base a una tabla de números aleatorios, de tal manera que una de las dos era colocada en el terrario ocupado por la otra. El criterio de cuál de los dos miembros de la pareja era la residente fue también por azar, y se utilizaron sólo aquéllas hembras residentes que habían pasado al menos 7 días en el terrario, ocupando normalmente el nido y comiendo allí.

Las observaciones tuvieron una duración mínima de 30 minutos, y hasta el final de la interacción en el caso de que ésta se produjera. El criterio de inicio y finalización de la interacción fue espacial. Se consideró que una interacción se iniciaba cuando la distancia que separaba a ambos animales era igual o inferior a 6 cm, existiendo orientación por parte de alguno de ellos hacia el otro, si las arañas se encontraban fuera del nido. Si la interacción se producía en el interior del nido, a partir del momento en que la intrusa apoyaba el primer par de patas en él. El criterio de finalización de la interacción fue el alejamiento a más de 6 cm

y pérdida de orientación por parte de una de las dos hembras, sin que existiera nueva orientación durante los 5 minutos siguientes.

Desde el inicio hasta el final de la observación, se registraron en cinta de video, fotografía seriada y por escrito todas las actividades y movimientos realizados por los animales, transcribiéndose posteriormente los datos. La intrusa era retirada tras el registro, no observándose un animal más de una vez en el mismo día.

De la observación de 73 parejas distintas, se obtuvieron un total de 33 secuencias de interacción. A partir de los datos obtenidos, se han descrito los patrones motores utilizados, el desarrollo y el resultado de las interacciones. Para cada interacción, se ha medido su duración en segundos, calculándose el valor medio, desviación standard y coeficiente de variación medido por:

$$C.V. = SD \times 100 / \bar{x}$$

Como variables independientes, se han controlado el tamaño de las dos hembras, su diferencia y la situación de residencia previa en la interacción. Para medir la dependencia entre el resultado y las variables individuales se ha utilizado una prueba de Chi cuadrado. En el caso de la variable "duración", se ha calculado el coeficiente de correlación, dado por:

$r = s_{xy} / S_x S_y$, siendo S_{xy} la covarianza entre x e y , y S_x , S_y las desviaciones standard de x e y , respectivamente.

RESULTADOS

Cuando se introduce a la hembra intrusa, se observa un periodo inicial de "adaptación" de alrededor de cinco minutos, durante el cual el animal que ha sido trasladado permanece inmóvil. Cuando inicia el movimiento, su comportamiento consiste en desplazamientos rápidos y erráticos por el terrario, con el cuerpo en posición erguida y próximo a las paredes, que intenta ocasionalmente escalar. No se observa direccionalidad aparente en estos desplazamientos.

En el curso de estos desplazamientos las hembras exhiben un movimiento de "sondeo" de palpos, y de "golpear con el primer par de patas". Tanto uno como otro movimientos no van acompañados de cambios en la dirección del desplazamiento con respecto a la posición del nido.

La localización de éste parece producirse por azar. Una vez en contacto con el brocal, la hembra realiza movimientos de palpos y del primer par similares a los mencionados anteriormente (Fig. 1), introduciéndose lentamente en el nido. Esta introducción se realiza con el primer par de patas extendido y con movimientos de los palpos sobre las paredes del nido (Fig. 2). Este patrón de comportamiento se ha observado en la introducción a cualquier nido, tanto si estaba ocupado como si no.

La residente suele permanecer inmóvil en el interior del nido ante el desplazamiento de la intrusa. En los casos en los que, por alguna razón, no lo ocupa o se encuentra sobre el brocal en el momento de iniciarse la observación, puede orientarse ante el movimiento de la otra araña a una distancia de hasta 25



Figura 1.—Sondeo de palpos de la hembra intrusa sobre el brocal. Se observa cómo la hembra pliega los palpos sobre un hilo de seda del brocal de un nido.



Figura 2.—Introducción de la hembra intrusa en el nido. Se observa el primer par de patas extendido y los palpos plegados sobre el brocal.

Tabla 1.—Tipos de interacciones agonísticas entre hembras. R = secuencias breves, en las que la interacción se resuelve rápidamente; L = secuencias largas, de resolución lenta.

Ocurrencia	N. inter.	Secuencias		Capturas
		R	L	
Dentro nido	27	9	18	6
Fuera nido	6	3	3	2
Total	33	12	21	8

cm, sea cual sea la posición relativa de ambas. En la Tabla 1 aparece reflejada la frecuencia con la que se han observado interacciones fuera y dentro del nido.

Cuando se encuentra en el nido, la hembra residente no se orienta hasta que la intrusa realiza movimientos sobre el brocal o se introduce en él. Esta introducción se realiza lentamente, y la orientación no suele producirse hasta que la distancia entre ambas se ha reducido a 3-5 cm. El comportamiento de la residente consiste en dar un salto hacia adelante en dirección a la intrusa con el primer par de patas extendido y elevado y los quelíceros abiertos, mostrando una pauta que hemos llamado “abalanzarse”.

Tras la embestida, algunas interacciones se resuelven rápidamente. En estos casos, a la embestida de la residente y tras el contacto frontal con el primer par de patas, puede seguir la huida de la intrusa o, en algunos casos, su captura. En otras ocasiones, la intrusa responde elevando a su vez el primer par de patas y abriendo quelíceros (Fig. 3). Se puede llegar a observar, en estos casos, un contacto de todas las patas (“traba”) similar al que se observa en la captura y



Figura 3.—Exhibición de quelíceros abiertos. En la parte superior se observa a la hembra intrusa con el primer par extendido y los quelíceros abiertos. En la parte inferior, se observa una exhibición de amenaza de la hembra residente.

sujeción de presas de gran tamaño, mostrando ambas arañas los quelíceros abiertos y repetidos intentos de morder a la adversaria. El resultado de la traba puede ser, de nuevo, la huida de una de las dos arañas o, en algunos casos, finalizar con la captura de una por parte de la otra (Tabla 1).

También puede, tras este primer contacto, producirse un retroceso por parte de la intrusa, aun permaneciendo en el interior del nido o sobre el brocal, con sucesivos intentos de aproximación. En estos casos en que la interacción no se resuelve rápidamente, el enfrentamiento se puede mantener hasta más de 8 horas, sucediéndose aproximaciones de la intrusa con el primer par de patas extendido hacia adelante, posiciones de inmovilidad con el primer par extendido y los quelíceros abiertos y "tamborileo de los palpos". En el interior del nido, la hembra residente suele permanecer inmóvil, manteniendo la posición de primer par extendido y elevado hasta la vertical y quelíceros abiertos ("amenaza"). Es de destacar que, en algunas ocasiones, se ha observado que en los momentos en que la hembra residente abandona esta posición, pierda o no la orientación hacia la adversaria, ésta intenta la introducción en el nido. En algunos casos, la distancia entre las dos hembras en este tipo de interacción es tan pequeña que se observa contacto directo y mantenido entre los quelíceros de ambas.

En estos casos la interacción se resuelve, también, tras un ataque, con la huida de una de las dos hembras o su captura (Tabla 1) permaneciendo la otra en el interior del nido; consideramos a esta última la vencedora en la interacción. Tan sólo en un caso se observó que las dos arañas se separaran quedando ambas en el interior del nido, una de ellas en el fondo y la otra sobre el brocal, no orientadas una a la otra. La hembra vencedora puede, incluso, perseguir a la otra hasta una distancia de dos o tres cm del brocal, manteniendo la orientación y la posición de amenaza hasta varios minutos.

Cuando las interacciones ocurren fuera del nido (Tabla 1), la aproximación de la residente a la intrusa se produce de forma escalonada, "a saltos", con el cuerpo en posición erguida y un avance casi simultáneo de las patas delanteras, en desplazamientos cortos, rápidos y en línea recta que recuerdan la aproximación a grandes distancias a presas de gran tamaño.

Cuando la distancia entre ambas se reduce a 3-5 cm, se puede producir la orientación de la hembra intrusa. Una vez ocurrida, el enfrentamiento entre ambas es frontal, desarrollándose la interacción en la forma descrita anteriormente en el interior del nido: suele resolverse tras el contacto y, en ocasiones, la traba, huyendo una de las dos arañas y permaneciendo inmóvil la otra, que mantiene durante algunos minutos la posición y la orientación. En otros casos, se observan sucesivas aproximaciones por parte de esta última, produciéndose repetidos contactos y huidas de la primera (Tabla 1).

En algunos casos, no hay orientación por parte de la hembra intrusa; puede huir, sin que haya contacto, ante la aproximación de la residente, o bien resultar capturada tras una embestida a corta distancia.

La comparación de las frecuencias de las secuencias R y L (Tabla 1) cuando la interacción tiene lugar dentro y fuera del nido da un $\chi^2 = 1.30$ ($\chi^2_{0.05,1} = 3.84$); la comparación de las frecuencias de captura en ambos contextos da un $\chi^2 = 1.00$.

La captura ha sido el resultado final de 8 de las 33 interacciones observadas. En 5 de estos casos, se produjo tras una interacción frontal larga, y en los otros tres tras aproximación lateral o posterior. En todos los casos, el resultado de la

Tabla 2.—Resultado de las interacciones en función de la residencia previa y del tamaño. VR = vence individuo residente; VI = vence individuo intruso; VM = vence individuo mayor; Vm = vence individuo menor.

Variable	Resultado	
Residencia	VR	24
	VI	9
Tamaño	VM	23
	Vm	10

captura fue la ingestión total de la congénere. Se observaron, además, cuatro intentos de captura en interacciones frontales que resultaron en la mordedura de alguna región no vital (patas) y la posterior separación de las arañas sin resultado final de muerte. En los otros 25 casos, el resultado final de la interacción consistió en la huida de una de las dos arañas.

En la Tabla 2 se indica cuál de las dos arañas resultó vencedora en función de las variables “residencia” y “tamaño”. Al aplicar una prueba de Chi cuadrado a los resultados de esta Tabla se obtiene que difieren del azar, tanto con respecto a la residencia $\chi^2 = 6.82, p < 0.05$), como al tamaño ($\chi^2 = 5.12, p < 0.05$).

En la Tabla 3 se presenta el resultado de las interacciones en función del tamaño de la residente. No existe dependencia significativa entre ambas variables $\chi^2 = 3.82$), aunque el valor obtenido está muy próximo al valor significativo ($\chi^2 = 3.84, p < 0.05$). Sin embargo, las arañas de mayor tamaño tienden a ganar más luchas cuando son residentes ($\chi^2 = 5.26, p < 0.05$).

La duración de las interacciones observadas es muy variable. El valor medio de la duración es de 2509.55 segundos, y su desviación standard 5254.16. Se ha calculado el coeficiente de correlación entre las variables “duración de la interacción” y “diferencia de tamaño” para el grupo en que el animal residente es el de mayor tamaño ($r = -0.36$) y el grupo en que el residente es el animal de menor tamaño ($r = -0.32$). Ninguno de estos valores es significativo estadísticamente ($p < 0.05$).

DISCUSION

El comportamiento exhibido por hembras adultas de *L. tarentula fasciiventris* en interacciones diádicas es similar al descrito por Nossek & Rovner (1984) en otras especies del género. La estrategia general, así como los patrones motores del

Table 3.—Resultado de las interacciones en función de las dos variables individuales.

Tamaño residente	Resultado		Total
	VR	VI	
Mayor	17	3	20
Menor	7	6	13
Total	24	9	33

comportamiento, no difieren tampoco, de forma significativa, de los descritos para los animales de este sexo y fase de desarrollo en otros contextos (Ortega 1985; Ortega et al. 1986). El nivel de especificidad de los patrones motores exhibidos es, por lo tanto, bajo, y menor que el observado en interacciones diádicas entre machos adultos en esta especie (Ortega et al. 1984).

El nivel de intensificación de las luchas es mayor que el observado, tanto en encuentros entre machos adultos de esta especie (Ortega et al. 1984), como en los descritos en otras especies (Nossek & Rovner 1984). Este hecho se traduce en el elevado índice de canibalismo observado.

La mayor parte de las interacciones se han registrado en el interior de los nidos, y su resultado consiste en el abandono de éste por parte de una de las dos hembras. Este hecho nos lleva a postular que estas interacciones pueden interpretarse como competitivas, siendo el recurso en litigio la ocupación de un nido. Dado el abrigo y la protección a temperaturas extremas que proporcionan (Humphreys 1987), puede tratarse de un recurso importante para la supervivencia de los individuos.

El elevado valor de este recurso podría explicar el alto nivel de intensificación que se observa en los encuentros estudiados. Se ha postulado, de hecho, que la intensificación de los encuentros se puede producir si el valor del recurso es muy alto (Maynard Smith & Parker 1976; Riechert 1982; Huntingford & Turner 1987).

No hemos detectado diferencias en la frecuencia de interacciones breves y largas o de capturas en función de que el encuentro se produzca o no en el interior del nido. En otros estudios no se ha detectado, tampoco, correlación entre la intensidad de la lucha y el valor del recurso (Hodge 1987).

El elevado riesgo de lesión como consecuencia de la intensificación podría haber llevado al desarrollo de estrategias de comportamiento que minimizaran los riesgos a los adversarios del tipo de "si eres residente ataca, y si eres intrusa huye" (Maynard Smith 1974; Hammerstein 1981). Esta hipótesis permitiría explicar la predictibilidad del resultado con respecto a la residencia que hemos observado. Sin embargo, no todas las interacciones se resuelven rápidamente en favor del individuo residente.

La existencia de contacto físico en la mayor parte de las interacciones podría indicar que la resolución de estos conflictos se produciría, básicamente, tras la evaluación de parámetros físicos del adversario (Turner & Huntingford 1986). Nuestros resultados concuerdan con la hipótesis de que el animal de mayores fuerza o tamaño tiene más probabilidades de resultar vencedor en estos encuentros (Aspey 1977; Riechert 1986).

La interacción de las dos variables de asimetría no queda clara a partir de los resultados obtenidos, aunque se observa una tendencia a que la probabilidad de vencer de la hembra residente sea mayor cuando es la de mayor tamaño. La variabilidad de las secuencias podría reflejar las diferentes situaciones en que se puede encontrar un animal en función del tamaño y residencia relativos, respondiendo las secuencias lentas a situaciones en las que las probabilidades de vencer de la intrusa, en función de su tamaño, fueran grandes, y las secuencias rápidas a los casos en que no fuera así. Estos planteamientos se ajustan a la tendencia a una correlación negativa que hemos observado entre las variables "diferencia de tamaño" y "duración de la interacción": las interacciones más

largas corresponden a las situaciones en las que la diferencia de tamaño es pequeña.

Estos resultados concuerdan con la suposición de que los animales utilizan las interacciones para obtener información acerca de su tamaño relativo. Planteamos que la interpretación funcional de los patrones motores exhibidos en este contexto no debería tanto suponer que son señales que informan de la especie y sexo del animal, permitiendo el reconocimiento intraespecífico y disminuyendo el riesgo de que se produzca una respuesta predatoria indiscriminada (Krafft 1982), como que son patrones que servirían a los individuos para evaluar la situación a la que se enfrentan.

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IS IT THE SIZE THAT COUNTS? PALP MORPHOLOGY, SPERM STORAGE, AND EGG HATCHING FREQUENCY IN *NEPHILA CLAVIPES* (ARANEAE, ARANEIDAE)

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ABSTRACT

This study investigated the relationship between male size and reproductive success in *Nephila clavipes*, a neotropical orb-weaving spider. Gröss and palpal size variation were examined in relation to copulatory behavior, sperm transfer/uptake, and utilization by the female. The effect of conductor breakage was also evaluated by assessing the timing of its occurrence and its influence on sperm transfer.

There was less variation in palp size of male *N. clavipes* than in other aspects of male morphology. Gross male body size correlated most highly with how much sperm was produced, transferred to, and stored by the female. Size of the male was not related, however, to the percentage of sperm actually transferred. The number of sperm retained by the female was influenced by the time of mating, but not by copulatory behavior. Approximately twice as many sperm were found in the palps of virgin males as were found in combined totals from mated pairs. This suggests that a substantial percentage of sperm transferred by the male is not stored by the female. None of the variables analyzed in this study greatly influenced the percentage of eggs eventually hatching. Conductor breakage seriously interfered with sperm transfer but occurred less often than expected and did not appear to result from copulatory activity.

INTRODUCTION

Individual differences in invertebrate male morphology may influence copulatory behavior (Jackson 1980; Thornhill and Alcock 1983; Christenson 1984). Male morphological variation may differentially affect internal processes in the female as well. Eberhard (1985) postulated that females in a wide variety of taxa may copulate with many males but discriminate based upon characteristics of the males' genitalia, fertilizing her eggs with sperm from the most desirable male. This might be accomplished through control of intromission, and differential uptake of sperm, among other mechanisms (Eberhard 1985). Once copulation has begun, females could monitor such variables as intensity or quality of stimuli received, thereby affecting the timing and consequences of copulation including uptake and storage (Jackson 1980; Thornhill and Alcock 1983; Eberhard 1985, 1986).

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The genitalia of male golden orb-weaving spiders (*Nephila clavipes* L.) are not noted for great complexity (Schult and Sellenschlo 1983). One outstanding characteristic, however, is the size of the conductor. Males of similar weight and/or body length, differing in conductor size, will almost certainly differ in the stimulation they provide the female, possibly affecting how much sperm is stored and later utilized by the female. Selective pressures determining conductor size could be open-ended, i.e., continuous pressure for ever larger (or smaller) size, or restrictive, i.e., males with an optimal genitalic size having an advantage over males with larger or smaller conductors. In this study, variation in *N. clavipes* palpal morphology was first assessed and compared to variation in more gross aspects of male size and sperm production. The relationships of natural and experimentally induced palp variation with transfer/storage, copulatory behavior, and egg hatching percentage were then evaluated. Because reproductive behavior of *N. clavipes* differs depending upon the age of the female (Christenson et al. 1985), palpal variation could have different effects on the uptake of sperm by young and mature adult females. Males were therefore mated with females either immediately following the final molt or two weeks post-molt.

METHODS

Study site.—The study was conducted at the F. Edward Hebert Center of Tulane University, approximately 20 km south of New Orleans in Belle Chasse, La. The facility is situated on 500 acres of hardwood, bottomland forest of elm, maple, oak, hackberry, and box elder. The site is transected by dirt roads, drainage ditches, and a series of lagoons.

Subject selection.—One hundred sixty-seven male and 157 female *N. clavipes* were collected at either the Hebert Center or the Barataria unit of Jean Lafitte National Historical Park in Barataria, La., in July and August 1987. Males were selected based upon coloration, web structure, and the presence of sperm webs, thus ensuring all were approximately the same age, that is, within one or two days after their final molt (Myers and Christenson 1988). Seventeen males, to be included in the virgin male analysis, were selected for very small size (less than 6 mm cephalothorax-abdomen length) or very large body size (greater than 9 mm). Those to be included in the two mated male studies were not selected for size. Females selected were between 18–20 mm in cephalothorax-abdomen length. This ensured that they were in their penultimate instar (Moore 1977). The spiders were housed in 123 × 62 × 62 cm boxes constructed of wood furring strips sided with Fiberglas® screening. Female subjects were presented one or two mealworm larvae each day.

Female *N. clavipes* were divided into four groups. The first variable was the female's age at mating: Day of final molt (Day 0) or two weeks post-molt (Day 14). The second variable, was the measure of reproductive success: Number of sperm found in female's sperm storage sacs (Sperm) or percent of clutch hatched (Egg). This resulted in a 2 × 2 (age vs measure) factorial design.

Initial palp evaluation.—In daily groups of approximately 20, 100 male subjects were brought into the lab before assignment to females. Males were subjected to hypothermia by placing them in a refrigerator for a few minutes and then checked for the occurrence of conductor breakage. Those found to have broken

conductor tips were excluded ($N = 4$). Males were not kept out of the field for more than 24 hours.

Mating procedure.—Males in the Day 0 groups were housed together until a female's web showed signs of degeneration, indicating a molt was to occur within a few days. At this time a male was randomly selected from the storage box (similar to female boxes) and placed via a stick near the hub position above the female. Among Day 14 dyads, virgin females were supplied with males 14 days after their final molt. After placing the male, a mealworm was added to the web to facilitate female receptivity (Christenson et al. 1985). Males in both conditions were rarely housed apart from females for more than two days.

Behavioral records.—Serial recording was conducted for a minimum of one hour on the day of the female's final molt in Day 0 females and following prey capture or the onset of copulation in Day 14 females (whichever occurred first). Specific behaviors recorded included amount of time spent *in copula* (min per h), the number of copulatory bouts (BOUT - the number of observed palpal insertions of at least 5 sec duration), rates of hematodochal bulb contractions (BC - mean rate per min), number of palp pounding bouts (PP - male rapidly drums his palps on epigynum of the female, 1 sec separating bouts), and number of female fends (FF). The latter was defined as any female behavior which either immediately terminated a copulatory bout or immediately caused a male to move off of or away from her venter. Fends generally included a brisk brushing of the male with the female's third pair of legs.

Subsequent analyses of male size.—Males were sacrificed by hypothermia. Wet weights were taken and measurements of cephalothorax-abdomen length (CthA) and tibia-patella length (TiPt) were made. Conductors were rechecked to determine frequency of breakage in non-virgin males. Palps were then removed. If not broken, the right palp was measured on a Quantimet 970 Image Analyzer®, otherwise the left palp was used. Four separate measures of palpal length were made (Fig. 1): 1. overall palp length along its retrolateral axis (PLRA); 2. length of conductor along its prolateral axis (CLPA); 3. length of conductor along prolateral axis below the conductor buttress (CLBB); 4. width of conductor at widest point (CndW). Gross and palpal measurements were taken twice on 10 males. Correlations between first and second measurements were greater than or equal to 0.98.

Some slight differences in morphology were found between males assigned to Day 0 and Day 14 females. As males were randomly assigned to these groups, and since both groups were run in equal numbers throughout the summer, these differences were likely due to chance. There were trends toward significantly larger tibia-patella length ($F_{1,135} = 3.20$; $p = .076$) and greater weight in Day 0 males ($F_{1,135} = 3.88$; $p = .051$). There was a tendency for Day 0 males to have larger conductors in three of four measures: PLRA ($F_{1,135} = 2.98$; $p = 0.086$), CLPA ($F_{1,135} = 3.52$; $p = 0.063$), CLBB ($F_{1,135} = 0.00$; $p = 0.973$), CndW ($F_{1,135} = 4.03$; $p = 0.047$).

Conductor manipulation.—To determine the effects of conductor breakage on copulatory behavior and sperm transfer/storage, conductor tips of 10 males were severed with a scalpel blade. The cuts were made approximately 0.2 mm from the distal end of the conductor, about the length which is occasionally broken off in nature. Males were maintained outdoors in separate boxes for two days after this procedure to await placement on a female's unrepaired web. Ten additional males

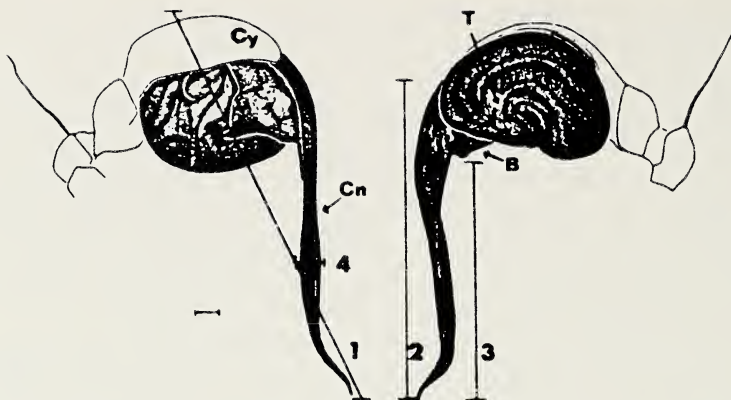


Figure 1.—Measurements of palp morphology. Retrolateral view on the left, prolateral on the right. 1 = PLRA - Palp length retrolateral axis, 2 = CLPA - Conductor length prolateral axis, 3 = Conductor length below buttress, 4 = CndW - conductor width at widest point (retrolateral axis), B = conductor buttress, Cn = conductor, Cy = cymbium; T = tegulum. Adapted from Levi (1980). Used by permission of the Museum of Comparative Zoology, Harvard University. Scale = 0.1 mm.

serving as controls were similarly handled but not cut. Females mated with these control males were part of the Day 0 Sperm group.

Histological procedure.—Mated pairs in the Sperm groups were brought into the lab five days following their initial copulation, ensuring that female sperm storage sacs had hardened. The storage sacs were removed under a dissecting microscope then placed in a 4 ml centrifuge tube with 200 μ l of Ringer's solution. Following analyses on the image analyzer, male palps were treated in the same manner. The palps (or sacs) were ground thoroughly with forceps and then vortexed for approximately one min. The tubes were then centrifuged for 25 min at 1000 g. The tubes were removed, and the grinding, vortexing, and centrifuging were repeated two more times. The tubes were vortexed one more time, and then 5 ml samples were immediately removed, placed on acid-cleaned gel-coated slides, dried overnight, and stained with hematoxylin. In the study of sperm availability in virgin males, the procedure was identical.

Sperm counts.—Sperm counts were performed on a Quantimet 970 Image Analyzer®. To facilitate counting, 5 ml samples were used (2.5 percent of the total). The image analyzer was programmed to count all objects with an area of between 3 μ^2 and 25 μ^2 . Within-field editing allowed for the exclusion of extraneous material.

Egg sac analyses.—Following mating, females in the Egg groups were maintained until oviposition. Egg sacs were brought into the lab approximately five weeks after oviposition, sufficient time for spiderlings to have hatched and molted to the second instar. Number of spiderlings, unhatched eggs, and egg sac parasites were counted.

RESULTS

Palpal and gross morphological variation among mated males.—Overall palp length (PLRA) ranged between 1.75 and 2.33 mm, a difference of about 25 percent. The distribution was normal with a skew of well under 1.00 (normality)

Table 1.—Mean (\bar{x}) and standard deviations (SD) for Day 0 and Day 14 subjects. The number of sperm found in the male has been omitted from Day 0 data, as only a few sperm were found in only two males. Sperm number refers to sample size (2.5% of the total) in Day 0 and Day 14 Sperm subjects ($n = 35, 36$ respectively). Percentage of clutch hatched refers to Day 0 and Day 14 Egg subjects only ($n = 31, 38$ respectively). PLRA = Palp length along retrolateral axis; CLPA = Conductor length along prolateral axis; CLBB = conductor length below buttress; CndW = Conductor width at widest point.

Measure	Day 0 ($n = 66$)		Day 14 ($n = 74$)	
	\bar{x}	SD	\bar{x}	SD
Cephalothorax abdomen (mm)	7.67	1.24	7.47	1.12
Tibia Patella (mm)	6.89	1.22	6.53	1.12
Weight (g)	0.033	0.016	0.028	0.010
PLRA (mm)	2.08	0.12	2.04	0.11
CLPA (mm)	1.60	0.07	1.58	0.08
CLBB (mm)	1.22	0.06	1.22	0.06
CndW (mm)	0.10	0.01	0.10	0.01
Sperm remaining in male palps	—	—	4401	4592
Sperm stored in females	8037	3682	1834	1404
Egg hatching percentage	0.90	0.24	0.88	0.27
<i>In copula</i> (min/h)	26.7	13.0	10.6	9.4
Hematodochal bulb contraction rate (n per min)	36.2	16.0	0.4	9.1
Female fends (per h)	21.4	16.2	1.7	7.0
Copulatory bouts (per h)	10.4	7.4	1.5	1.4
Palp pounds (bouts per h)	25.9	21.2	3.1	4.9

in Day 0 and Day 14 males. In comparison, tibia-patella length varied by over 100 percent, ranging between 4.0 and 9.4 mm. Indices of skewness and kurtosis exhibited trivial differences from normality between all morphological measures. Means and standard deviations for morphological and behavioral data are presented in Table 1.

Palps were less variable than more general measures of body size. This was determined by calculating coefficients of variation (standard deviation/(mean \times 100)) and testing for significance using log transformations of each of the morphological variables in Day 0 and Day 14 males. Log transformation allowed the variance of each variable to be compared directly (Lewontin 1966). An F -ratio was formed between the coefficient for each palp measure and each gross morphological measure. Coefficients for palp measurements were significantly smaller than those for weight, tibia-patella length, or cephalothorax-abdomen length ($p < 0.007$). Among gross morphological variables, the coefficient for weight was significantly larger than that for tibia-patella length or cephalothorax-abdomen length ($p < 0.001$). Coefficients and variance of log transformed data are presented for Day 0 and Day 14 subjects in Table 2.

There was a positive correlation between palp size and gross body size. The highest correlation found was between PLRA and tibia-patella length in Day 14 subjects ($r = 0.82$; $p < 0.00001$).

Male size and available sperm in virgins.—In virgin males, the amount of sperm found in palps was highly related to gross and palpal morphology. The highest correlation was with weight ($r = 0.82$; $p < 0.0001$) and the lowest was with tibia-patella length ($r = 0.72$; $p = 0.002$). The various measurements of palp structure correlated equally with the amount of available sperm. Variables PLRA, CLBB, and CndW correlated with sperm at $r = 0.75$ or 0.76 ($p < 0.002$). Variable

Table 2.—Coefficients of variation (C. V.) (Mean/(Standard deviation X 100)) and variance of gross morphological and palpal measures using log transformation. CthA = cephalothorax-abdomen length; TiPt = Tibia-Patella length; PLRA = Palp length along retrolateral axis; CLPA = Conductor length along prolateral axis; CLBB = conductor length below buttress; CndW = Conductor width at widest point.

Measure	Day 0		Day 14	
	C. V.	$s^2(\text{Log}(x))$	C. V.	$s^2(\text{Log}(x))$
Gross				
CthA	15.84	5.18×10^{-3}	15.03	4.36×10^{-3}
Weight	50.05	6.56×10^{-3}	45.05	5.62×10^{-3}
TiPt	19.05	8.12×10^{-2}	17.30	4.04×10^{-2}
Palp				
PLRA	6.06	6.76×10^{-4}	5.33	5.29×10^{-4}
CLPA	4.62	4.00×10^{-4}	4.91	4.41×10^{-4}
CLBB	5.01	5.29×10^{-4}	4.90	4.41×10^{-4}
CndW	7.11	5.29×10^{-4}	7.71	4.41×10^{-4}

CLPA correlated with sperm at $r = 0.61$ ($p = 0.009$). Selection bias for very large and very small males resulted in somewhat exaggerated Pearson's r s.

Male size and sperm storage by females.—Male weight was the best predictor, among male morphological characteristics, of the amount of sperm stored by the female. Stepwise multiple regression performed on collapsed Day 0 and Day 14 data yielded a multiple R of 0.31 for the variable WGT. This score accounted for a significant amount of the variance ($F_{2,68} = 7.42$; $p = 0.001$). The variable CthA accounted for a significant proportion of the remaining variance. When included in the equation, CthA increased the multiple R to 0.41 ($F_{2,68} = 6.84$; $p = 0.002$). The relationships between male weight and the amount of sperm stored by the female in Day 0 and Day 14 dyads are presented in Fig. 2.

Male size and proportion of sperm transferred.—When the amount of sperm found in the female was expressed as a percentage of the total available sperm in the female (SP-F) and male (SP-M) combined (SP-F/(SP-M + SP-F)), no significant relationships were found between the proportion of sperm found in the female and any aspect of male morphology. To test whether males with average-sized palps had an advantage over males of either extreme, proportions of sperm transferred from Day 14 males were converted to z -scores and Pearson r s calculated for the four palpal variables vs the z -scores' absolute values. Once again, no significant relationship was found.

Male size and copulatory behavior.—To examine whether small males exhibit differences in copulatory behavior to compensate for a deficit in the ability to facilitate sperm storage, the 10 largest (M CthA = 9.50; SD = 0.81) and 10 smallest (M CthA = 5.90; SD = 0.43) males were selected from the Day 0 groups and the 11 largest (M CthA = 9.20; SD = 0.38) and 11 smallest (M CthA = 6.00; SD = 0.57) from the Day 14 groups. Each group was divided in half again based upon palp size (large or small palps using PLRA as an index), resulting in a 2×2 body size vs palp size design. Two-way analyses of variance were conducted to determine whether these divisions resulted in significant size differences.

Day 0 subjects.—As expected, big males had significantly larger palps than small males ($F_{1,16} = 196.904$; $p < 0.0001$). When the data were collapsed across body size, a significant difference was still found between the largest and smallest

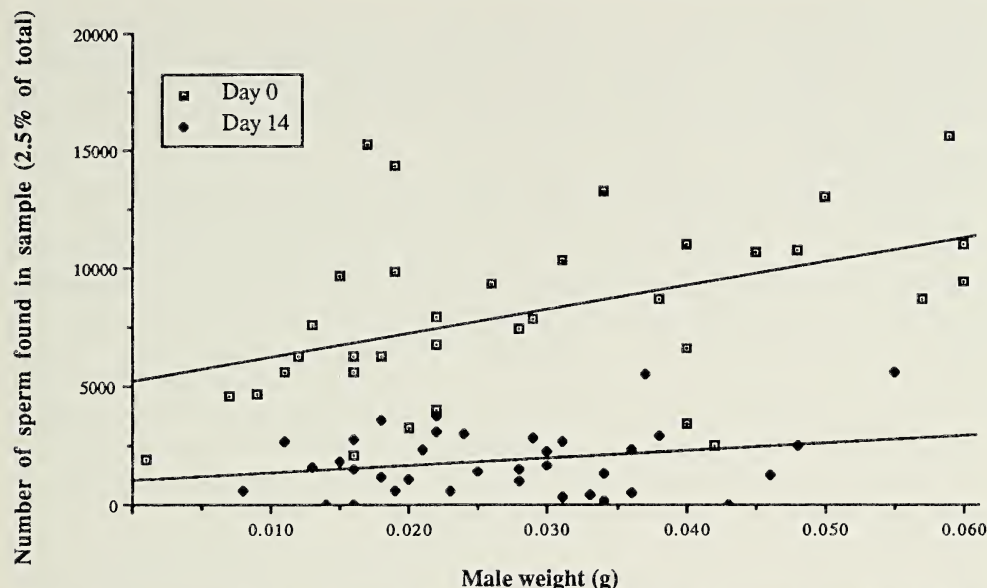


Figure 2.—Scatterplot for male weight (g) and sperm (samples) found in female storage sacs in Day 0 and Day 14 dyads with regression lines. Pearson r for Day 0 animals = 0.46 ($p = 0.0002$). Regression equation is $Y = 5125 + 1.0163e+5x$. For Day 14 animals the correlation is 0.25 ($p = 0.05$) and the regression equation is $Y = 991.1 + 3.1331e+4x$.

palps (PLRA, large bodied males, $M = 2.12$; $SD = 0.05$; PLRA, small bodied males, $M = 1.81$; $SD = 0.04$; $F_{1,16} = 44.109$; $p < 0.0001$). The palp size \times body size interaction was not significant ($p < 0.267$). No behavioral differences related to palp size or body weight were uncovered using MANOVA.

Day 14 subjects.—Large and small males displayed means and differences in palp size nearly identical to those found in Day 0 males. Higher rates of some copulatory behaviors were observed in larger males during the one hour serial record: COP ($F_{1,18} = 5.98$; $p < 0.025$), BOUT ($F_{1,18} = 4.77$; $p < 0.043$), PP ($F_{1,18} = 7.82$; $p < 0.012$). The overall multivariate F of behavioral differences based on male weight was significant ($F_{6,13} = 3.83$; $p = 0.02$). Higher rates of palp pounding in large-palped males ($F_{1,18} = 18.58$; $p < 0.0004$) and more copulatory bouts ($F_{1,18} = 4.77$; $p < 0.043$) contributed to a trend towards significance in the multivariate F of differences based on palp size ($F_{6,13} = 2.74$; $p = 0.06$). The overall multivariate F for the palp size by body weight interaction was not significant ($p = 0.34$).

Male size and egg hatching.—Hatching percentage was not dependent upon the size of the male. The highest correlation was with cephalothorax-abdomen length in Day 0 subjects ($r = 0.25$; $p = 0.05$). This relationship was not apparent in the Day 14 Egg group.

Female age at mating, sperm storage, and copulatory behavior.—When mating with a newly-molted female, males nearly always transferred their entire supply of sperm ($M > 99$ percent). When copulation was delayed for two weeks, mated males retained about 24 percent of the sperm found in virgin males. A one-way analysis of variance between Sperm groups indicated that significantly more sperm were found in Day 0 females ($F_{1,69} = 35.70$; $p < 0.0001$). A mean of 8037 sperm was found in Day 0 samples ($SD = 3682$), versus 1834 in Day 14 samples

(SD = 1404). These means reflect sample sizes of 2.5 percent of the total sperm. When the number of sperm transferred to Day 14 females was expressed as a percentage of the total available sperm ($SP-F/(SP-M + SP-F)$), no relationship was found to exist between any of the behavioral variables and the proportion of sperm transferred.

A MANOVA was performed to determine if any aspects of copulatory activity were related to female age at mating. Due to missing data, three dyads were dropped (for this analysis only) leaving a total of 137. The overall multivariate F was significant ($F_{14,122} = 24.75$; $p < 0.0001$), indicating that the overall pattern of variable scores differed between Day 0 and Day 14 subjects. Subsequent analyses revealed significantly higher rates of copulatory activity in Day 0 subjects: more time spent copulating per one hour serial record ($F_{1,135} = 68.87$; $p < 0.0001$), a higher number of copulatory bouts ($F_{1,135} = 105.79$; $p < 0.0001$), higher rate of hematochochal bulb contractions ($F_{1,135} = 143.50$; $p < 0.0001$), and more palp pounding ($F_{1,135} = 77.40$; $p < 0.0001$). There were more fends by the female as well ($F_{1,135} = 87.73$; $p < 0.0001$).

Females fended males more often per unit time spent copulating on Day 0 ($F_{1,115} = 10.498$; $p < 0.002$); the mean fend/cop ratio was 1.04 on Day 0 versus 0.33 on Day 14. Cases where no copulations were observed during the one hour observation period were dropped from this analysis ($N = 23$) leaving a final N of 117. To determine if females were influencing the number of times a male attempted to mate, 10 Day 0 dyads and 10 Day 14 dyads were randomly selected from those dyads in which at least one mating attempt and fend were observed. The above analysis was then repeated using the ratio of fends to copulatory attempts. A copulatory attempt was defined as occurring when the male descended to the ventrum of the female followed by either successful copulation or insertion of less than 5 sec. No significant difference was found between Day 0 and Day 14 dyads ($p = 0.346$). Day 0 males were fended a mean of 1.1 times per copulatory attempt. Day 14 males were fended a mean of 0.8 times per attempt.

Do females influence copulation duration?—Gross female activity had little effect on male reproductive behavior. Female fends of males were not correlated with the amount of copulation and only a slight negative correlation was found with the amount of sperm later obtained in the female (Day 0 $r = -0.23$; $p = 0.06$; Day 14 $r = -0.26$; $p = 0.05$). Fends were positively correlated with BC rates in Day 0 males ($r = 0.38$; $p = 0.001$), but this relationship was not found in Day 14 dyads.

Copulatory behavior and sperm storage.—Among Day 0 subjects, total copulation time was the best behavioral predictor of the amount of sperm found in the female. This variable had a correlation with SP-F of 0.47, and was the only variable accounting for a significant proportion of the total variance ($F_{1,32} = 8.89$; $p < 0.001$). No behavioral variables were related to the amount of sperm found among Day 14 females. The predictive value of behavioral variables were determined by stepwise multiple regression analysis. Because of behavioral differences between Day 0 and Day 14 mating, the analysis was run under each condition.

Amount of sperm transferred during feeding bouts.—Day 14 Sperm dyads were analyzed to determine how much sperm were transferred during each mating bout. These copulations took place almost exclusively after mealworms were added and when females were observed feeding. The numbers of bouts are only

an approximation as clearly not every one occurring within these dyads was recorded. In three cases, sperm were found in females even though no copulation was observed. Because final molts were observed, it is clear that insemination could only have been carried out by the introduced males. These dyads were included and scored as having the minimum possible one copulatory bout. A mean of 2.8 copulatory bouts were observed among Day 14 Sperm subjects over the 4 days of observations ($SD = 1.6$). Each bout resulted in the transfer of a mean of 37 750 sperm ($SD = 46\,886$). These were the true numbers, obtained by multiplying the sample size by 40. As the mean amount of sperm found in virgin males (total, not sample size) was 520 898 ($SD = 257\,779$), each bout transferred about seven percent of the male's total sperm. There was, however, a large amount of variation among males.

"Lost" sperm.—Because the combination of SP-F and SP-M always appeared to be less than the amount of sperm found in similarly-sized virgin males, a comparison was made between the two totals. Seventeen mated males were matched for weight with the virgin males. Virgin males contained significantly more sperm than were found in mated pairs ($F_{1,34} = 17.64$; $p = 0.0002$). There was a mean of 13 022 sperm in the virgin male samples ($SD = 6444$) and 6261 in the mated pair samples ($SD = 2647$). There was no significant difference in weight between the mated and virgin males ($M = 0.029$ g and 0.021 g, respectively), hence a reasonable matching ($p = 0.30$).

Copulatory behavior, time of mating, and egg hatching.—Egg hatching percentage was not greatly influenced by male behavior. The highest correlation found was with hematochal bulb contraction rate ($r = 0.25$; $p = 0.05$). This correlation was identical for both the Day 0 and the Day 14 groups. Females of both groups had a mean 89 percent of their clutch hatch. Time of mating did not affect egg hatching percentage ($p = 0.727$).

Differences in egg parasitism between Day 0 and Day 14 clutches.—Many egg sacs contained parasites. The majority were larvae of the insect family Mantispidae. One sac contained a small unidentified spider. Twelve of 31 Day 0 egg sacs (39%) were found to contain at least one parasite. Nine of 38 Day 14 egg sacs (24%) were also parasitized. Chi-square analysis indicated no significant association of time of mating with rates of egg parasitism ($p = 0.177$).

Frequency of conductor breakage.—Only the first 100 virgin males collected for this study were checked for broken conductors prior to their introduction to females. Four had a broken conductor tip and were excluded. When the 140 mated males included in this study (excluding those that were artificially broken) were examined, eight had a single broken conductor. No males had two broken conductors. Chi-square analysis indicated that conductor breakage was equally likely in virgin and non-virgin males ($p = 0.54$). Chi-square analysis further indicated that, following mating, sperm remaining in males with broken conductors equalled that of intact males matched for weight and time of mating ($p = 0.59$). As conductors were not found to be broken more frequently following mating, it is clear that copulation is not a major cause of conductor breakage.

Cut palp study.—Severing the tips of conductors had adverse effects on male reproductive behavior. Hematochal bulb contractions, an index of copulation intensity, were observed in only two of the experimental males tested. A small amount of sperm (about 250/sample) were found in one female paired with a cut male. A MANOVA was performed to evaluate differences in copulatory behavior

between these two groups. The overall multivariate F was significant ($F_{9,9} = 9.49$; $p = 0.001$). Intact males were observed copulating significantly more often than cut palp animals ($F_{1,17} = 29.08$; $p < 0.0001$). Hematodochal bulb contractions were significantly faster in intact males as well ($F_{1,17} = 7.31$; $p = 0.015$). The damaged palp was clearly preventing successful copulation. This was also reflected in the number of copulatory bouts ($F_{1,17} = 19.73$; $p = 0.0004$). Motivation to mate, however, seemed unaffected. The number of copulatory attempts made by the males were compared to evaluate whether damaged males were less active. There was no significant difference between intact and cut palp males ($p = 0.65$) nor were differences in palp pounding observed ($p = 0.19$). Females did not distinguish between intact and damaged males. Cut palp males were not fended away any more often than intact males ($p = 0.12$). Behavioral data for cut palp and intact males are presented in Table 3.

DISCUSSION

Palpal Variation and its relation to gross male morphology.—Variation in palp size does not exhibit a range comparable to that found in more gross measurements such as weight or cephalothorax-abdomen length. Small males with exceptionally large palps or large males with small palps were not observed in the sample studied. The reduced variance in palpal size is consistent with results obtained in other genera such as *Pardosa* (Barnes 1959), *Castianeira* (Reiskind 1969), and *Hypochilus* (Coyle 1985). This consistency is an important reason for the use of male genitalia as taxonomic markers (McCrone 1963; Coyle 1985), and suggests that any selective forces at work favor a narrow range of palp sizes rather than a trend towards ever larger (or smaller) palps. While there are likely to be genetic constraints on the overall size of males, there appear to be stronger constraints on palp size. Ecological variables such as prey availability and temperature exert a much stronger influence on gross morphology than on palp morphology (Vollrath 1980). Growth rates among unrestrained populations during critical periods of development are highly variable, changing with shifts in these factors (Coyle 1985).

Determinants of sperm storage by males and females, and its utilization.—The amount of sperm stored in male palps prior to mating is closely related to overall male size. The correlation between size and sperm availability could be due to two factors. Larger males probably have more gonadal tissue with which to manufacture sperm and larger palps in which to store sperm until the opportunity to mate arises.

The amount of sperm stored by female *N. clavipes* is related to the gross size of the male and to the size of his palps. When the amount of sperm found in Day 14 females was expressed as a percentage of the total, however, no advantage was found for exceptionally large, small, or average-sized males. As a large proportion of the available sperm was "misplaced" somewhere between copulation and laboratory analysis, this statement is made with some caution.

Twice as many sperm were present in virgin males as were later recovered from mated dyads. Some of the difference in numbers can be attributed to experimental procedures as the SP-M + SP-F group went through the sperm counting procedure twice and the virgin male group once. Sperm taken from

Table 3.—Descriptive statistics for intact and cut palp males in the conductor manipulation study. N = 19. \bar{x} = Mean; SD = Standard deviation.

Measure	Intact palp		Cut palp	
	\bar{x}	SD	\bar{x}	SD
Copulatory attempts (per h)	21.67	13.13	19.22	20.36
Palp pounds (bouts/h)	32.67	33.46	15.90	18.73
<i>In copula</i> (min per h)	22.00	11.47	1.67	3.54
Copulatory bouts (per h)	8.33	5.20	0.80	1.32
Hematodochal bulb contraction rate (n per min)	34.00	16.08	11.00	22.51
Female fends (per h)	23.00	20.37	10.78	14.65

females also had a tendency to clump together occasionally, sometimes making an accurate count more difficult. However, the very large difference indicates some loss of sperm and warrants further investigation.

Male body size, palp size, and behavior were not related to the percentage of eggs hatching. This is logical as females were not mated with second males and may be expected to use any sperm available to them at the time of oviposition. It remains to be seen whether the aforementioned variables influence paternity when females mate with more than one male.

Timing of the initial copulation.—The timing of mating greatly influences copulatory behavior and the amount of sperm ultimately stored by the female. These results are consistent with past studies of *N. clavipes* (Brown 1985; Christenson et al. 1985). There was no reduction in female reproductive success when her initial mating was delayed for two weeks. Surprisingly, females fended off males significantly more often just after molting. This is in part due to the increased amount of copulatory behavior occurring at this time. When the proportion of fends to observed copulation time is compared for the two groups, however, it is clear that females were more reactive following the final molt.

Females in the Day 14 Egg group fertilized their entire clutch despite receiving only 24 percent of the males' sperm. This is interesting as it calls into question why a male transfers his entire supply of sperm when mating with a newly-molted adult. Some recent modeling by T. E. Christenson and W. P. Dunlap (Pers. comm.) proposes that total sperm transfer is the best strategy for a male mating with a newly-molted adult. Their model suggests that total transfer may be a consequence of the extended copulation necessary to insure a first male precedence effect (Christenson and Cohn 1988). One advantage may be to dilute the effectiveness of subsequent mating by the female. Sperm "dumping" may also result from the rather low probability of successful copulation (about 20 percent of males) and the even lower probability of a mated male either making it to the hub of another receptive female or defending his mated partner until oviposition (unpublished data).

Conductor breakage.—Conductor breakage did not occur in mated males at a higher rate than in virgins. The overall rate of breakage was low, less than seven percent. While the occasional broken conductor tip may inhibit further sperm uptake, the low rate of breakage suggests that this is not a typical occurrence. When conductor tips were experimentally severed, behavioral deficits were observed. Males with severed conductors did not mate successfully as only one male transferred a small number of sperm. Motivation to mate seemed unaffected

as there were no significant differences in the number of copulatory attempts or palp pounds.

Male copulatory behavior, morphology, and uptake.—The copulatory behaviors evaluated in this study did not vary systematically with either male size or uptake of sperm by the female. Hematodochal bulb contraction rates were higher in Day 0 males, and females in this group acquired more sperm. These differences seem to be related to the softer, unsclerotized epigynal tissues in newly-molted females and not to individual male variation (Christenson and Cohn 1988). Among Day 0 subjects, copulation time correlated most strongly with the number of sperm found in the female. This is surprising as all males in this group were virtually depleted of sperm. These results, and the finding that a good deal of sperm may be “lost”, suggest that increased amounts of copulatory activity could facilitate storage of sperm and not just release. However, no relationship was found between observed copulation time and the amount of sperm later found in Day 14 females. These results suggest that larger amounts of sperm simply take longer to transfer. In *N. clavipes*, however, all sperm is transferred within the first three hours while copulation continues for up to 48 h (Christenson and Cohn 1988). It seems unlikely, therefore, that the higher proportion of time larger males spent *in copula* was due to the volume of sperm they carried. The meaningfulness of the relationship between copulation time and sperm storage by the female remains unclear. Twenty-four h serial records need to be conducted on older adult females mating for the first time, with sampling of the amount of sperm found in each member of the dyad occurring at different times after the first observed copulation. Time sampling methodology as employed in the present study may not be able to yield data of sufficient accuracy.

Sexual selection in *N. clavipes*.—The following conclusions can be drawn regarding sexual selection in *N. clavipes*. Intense intrasexual selection, through agonistic encounters among males, takes place before, during, and after copulation (Goist 1983; Cohn et al. 1988). No evidence for intersexual selection was found in the present study. This investigation was, however, conducted within very narrow parameters, during and immediately after mating with a single male. Female *N. clavipes* can, of course, influence their reproductive processes in ways not addressed in the present study. For example, Christenson and Cohn (1988) demonstrated that the first male advantage typical in *N. clavipes* can be significantly reduced if males are limited in the amount of copulation time following sperm transfer. Post-transfer copulation may reduce future sexual receptivity in the female (Christenson and Cohn 1988). Fifteen percent of females leave their orb within 24 h of their final molt with little likelihood of successful pursuit by the male (Cohn et al. 1988). These early departures may provide a means for intersexual selection to operate.

In summary, a close relationship was found between the size of the male, the amount of sperm available for transfer, and the amount of sperm later found in the females' storage sacs. Females who mate with the largest males store the most sperm, but even the smallest males transfer enough to fertilize a clutch. While female *N. clavipes* may exercise several reproductive options, no preference for males of a particular size was found within the parameters of this study.

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THE SIZE OF SPIDER EGGS AND ESTIMATES OF THEIR ENERGY CONTENT

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ABSTRACT

Egg size was used to estimate the energy incorporated into egg production in a sample of 24 species representing 11 families. Egg mass scaled geometrically to egg diameter. Egg mass can be accurately estimated from the easily measured diameter of an egg. Comparison of egg sizes between populations of seven species common to Connecticut and Florida suggest egg size is species-specific. The constancy of energy density of spider eggs allows relatively accurate estimates of the energy incorporated into egg production using easily obtained data on egg size, number of eggs per clutch, and number of clutches.

INTRODUCTION

A basic consideration in most studies of spider reproduction relates egg production to energy availability (Craig 1987). In general, the number of clutches and number of eggs per clutch is determined by food supply (Bristowe 1958; Riechert and Tracy 1975; Enders 1976; Eberhard 1979; Craig 1987).

Studies emphasizing energetic costs of producing eggs exhibit a potential problem, namely the difficulty of measuring all the components necessary to estimate such costs. Single indices such as egg number (Petersen 1950; Enders 1976; Valerio 1976; Miyashita 1987a,b; Roach 1988; DeKeer and Maelfait 1988) and egg mass (Taylor and Peck 1975; Riechert and Tracy 1975; Killebrew and Ford 1985; Morse 1987) have been used as estimates of the energy incorporated into egg production. Use of single indices requires certain assumptions to make valid comparisons. For example, comparison of egg number assumes egg sizes are equal among the compared groups. A complete estimate of such costs over the life span of a female spider requires data on the number of clutches, the number of eggs per clutch, egg size, and energy density of the eggs. The fact that these studies are incomplete in this context is evidence of the very real difficulties of obtaining such data.

A major problem in this context is measurement of energy density. Accurate estimates using bomb calorimetry are time consuming and require skill, dedication, and careful attention to numerous procedural details (Phillipson 1964; Paine 1971; Anderson 1978). The time and labor involved justifies search of other methods of estimating relative energy content of eggs. Analysis of inter- and intraspecific variation of clutch size, egg size, and energy density indicate the

latter is the least variable (Anderson 1978). Killebrew and Ford (1985) argued that mass per newly hatched spiderling, and by extension, egg mass, in any one species is "optimized by natural selection." If correct, egg size might provide a practical and reasonably accurate measure of the energy content of a spider egg.

Here I evaluate egg size, measured as a linear dimension, to estimate egg mass. Linear dimensions of eggs can be easily and accurately measured using dissecting microscopes common to most laboratories. My specific aims were to determine whether egg size is species-specific and, if so, to describe the relationship between diameter and egg mass.

METHODS AND MATERIALS

Egg sacs of various species were collected from habitats around Gainesville, Florida. Although I picked species based on availability of reproductively active females, some effort was made to choose those which provide a reasonable range in the measured parameters. Of the 24 species considered here, data for 12 were obtained from a previous study (Anderson 1978).

Eggs were removed from egg sacs and counted. Their total wet mass was immediately measured to the nearest 0.1 mg and the average mass per egg determined by calculation. Egg diameter was measured to the nearest 0.01 mm with a dissecting microscope fitted with a calibrated ocular on a minimum of ten eggs per egg sac. Since few eggs are exactly spherical, the reported diameters represent the average of measurements made on the longest and the shortest axis of an egg. Differences between these two measurements of all samples averaged 7%.

Assuming geometric similarity obtains, i.e., shape and density are constant, the mass of an egg would be proportional to diameter³ where the latter represents a characteristic linear dimension (McMahon and Bonner 1983). Consequently I fitted the data to the power function $EM = aED^b$. Here EM represents egg wet mass; ED is egg diameter; a is a proportionality constant and b is the exponent of the function. The parameters a and b were calculated by least squares analysis of paired data after transformation to common logarithms. Correction for bias in log-transformed data (Sprugel 1983) made in estimating the proportionality constant (a) produced a result not different from the uncorrected value. The standard error (S_b) and 95% confidence limits for b , r^2 , and $Sy \cdot x$ were calculated as indices of fit of the regression as recommended by Smith (1984).

RESULTS AND DISCUSSION

The data collected from 24 species representing 11 spider families (Table 1) show much variation. The largest female is 112 times the smallest in the sample; number of eggs per clutch, egg diameter, and egg mass exhibit 39-, 2.8-, and 17.5-fold variation in these measures, respectively.

A good fit exists between egg mass and egg diameter (Fig. 1). The coefficient of determination (r^2) is 0.99 and indicates the fraction of variation in egg mass explained by variation in egg diameter. The standard error of the estimate ($Sy \cdot x$), standard error (S_b) and 95% confidence limits for b are 0.035, 0.066, and 2.77-3.05, respectively. Support for the predictive ability of the model is provided by

Table 1.—Number, size, and mass of spider eggs. Data are averages (+/- SD).

FAMILY Species	Sample size (clutches)	Female live mass (mg)	Number of eggs per clutch	Egg diameter (mm)	Egg live mass (mg)
FILISTATIDAE					
<i>Filistata hibernalis</i>	14	347 (188)	129 (63)	1.37 (0.05)	1.42 (0.01)
<i>Physocyclus</i> species	3	28.9 (8.0)	73 (9.2)	0.82 (0.01)	0.31 (0.03)
THERIDIIDAE					
<i>Achaearanea tepidariorum</i>	5	37.7 (19.3)	149 (55)	0.59 (0.01)	0.12 (0.01)
<i>Argyrodes trigonum</i>	2	10.9	42	0.67	0.17
<i>Tidarren sisypoides</i>	1	51.8	238	0.66	0.16
ARANEIDAE					
<i>Acanthepeira stellata</i>	2	596	574	1.04	0.55
<i>Acanthepeira venusta</i>	5	182 (72)	232 (70)	0.88 (0.02)	0.34 (0.02)
<i>Argiope aurantia</i>	2	752	978	0.92	0.46
<i>Gasteracantha elipsoides</i>	1	175	195	0.81	0.25
<i>Mecynogea lemniscata</i>	7	59.9 (11.1)	25 (5.3)	1.01 (0.01)	0.54 (0.04)
<i>Metazygia wittfeldae</i>	5	87.0 (29.9)	84 (31)	1.06 (0.07)	0.51 (0.08)
<i>Nuctenea cornuta</i>	5	263 (52)	484 (130)	1.00 (0.02)	0.49 (0.05)
AGELENIDAE					
<i>Agelenopsis barrowsi</i>	1	138	60	0.98	0.47
PISAURIDAE					
<i>Pisaurina mira</i>	3	293 (78)	264 (207)	1.15 (0.09)	0.78 (0.09)
LYCOSIDAE					
<i>Lycosa lenta</i>	6	1007 (234)	302 (48)	1.45 (0.05)	1.59 (0.15)
OXYOPIDAE					
<i>Peucetia viridans</i>	5	348 (22)	382 (36)	1.48 (0.02)	1.77 (0.08)
SPARASSIDAE					
<i>Heteropoda venatoria</i>	1	1221	184	1.66	2.10
THOMISIDAE					
<i>Misumenoides formosipes</i>	1	117	552	1.01	0.47
<i>Misumenops celer</i>	1	28.1	73	0.78	0.25
SALTICIDAE					
<i>Eris marginata</i>	1	43.1	59	0.93	0.37
<i>Phidippus audax</i>	4	223 (29.3)	186 (69)	1.26 (0.05)	1.03 (0.09)
<i>Phidippus pulcherrimus</i>	4	75.1 (9.0)	76 (15)	1.25 (0.01)	1.00 (0.08)
<i>Phidippus regius</i>	1	570	439	1.29	1.17
<i>Thiodina sylvana</i>	2	44.9	70	1.08	0.69

Wise's (1973) data on egg dimensions of *Linyphia marginata*. Given the reported diameter for these eggs, the equation (Fig. 1) predicts a wet weight equal to that indicated.

Although egg size exhibits much variation interspecifically (Table 1), I was impressed by the constancy of this measure within a species (see also Anderson 1978; Killebrew and Ford 1985). For example, the coefficients of variation involving egg diameter *within* each of the 12 species where multiple samples were available average 3.0% (Table 1). Conversely, the coefficient of variation for average egg diameter of the same 12 species is 24.3%. If egg size is species-dependent and not subject to environmental influences, egg sizes of the same species from different populations should not differ from one another. Such a comparison was made using the appropriate data from Kaston (1981) for Connecticut populations of seven species in common (Table 2). Analysis of the paired data indicate no significant differences exist ($P = 0.94$) in egg size. The

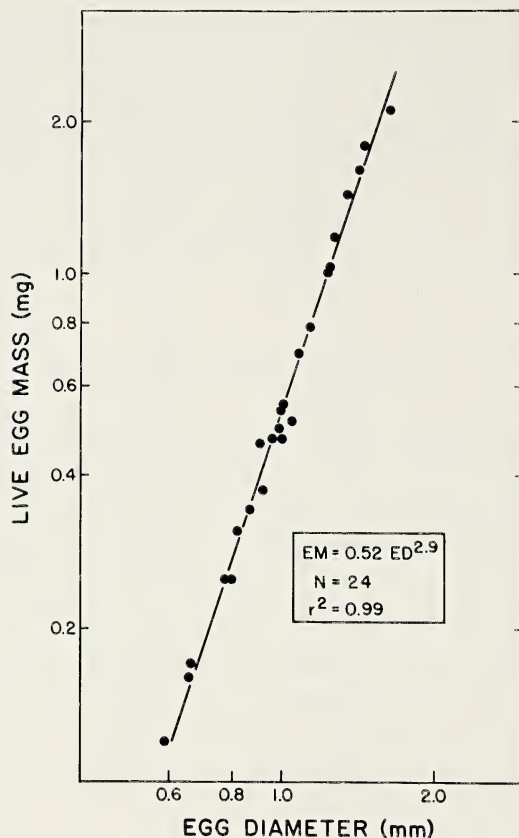


Figure 1.—Relationship between wet mass of egg (EM) and egg diameter (ED).

constancy of egg size provides validity to those studies comparing numbers of eggs or total egg mass as is so common in intraspecific studies.

The accuracy of estimates of the amount of energy incorporated into egg production made from number of clutches, number of eggs and their weight would depend on variation in energy density of eggs. Although variation in this measure is biologically significant and is correlated with the early life history patterns of individual species, the magnitude of this variation is not large (Anderson 1978). The reported values for the 12 species studied range from 26.3 to 29.0 joules per mg ash-free dry weight with an average of 27.3. Dry weight and

Table 2.—Comparison of egg size in spiders from Connecticut (Kaston 1981) and Florida (this study).

Species	Egg diameter (in mm)	
	Connecticut	Florida
<i>A. tepidariorum</i>	0.55	0.59
<i>A. trigonum</i>	0.65	0.67
<i>A. aurantia</i>	1.00	0.92
<i>N. cornuta</i>	1.00	1.15
<i>P. mira</i>	1.20	1.15
<i>M. formosipes</i>	0.96	1.01
<i>P. audax</i>	1.22	1.26

ash content of spider eggs are 31.9 and 3.58% of wet weight, respectively (Anderson 1978). Relative to the average, the potential error associated with the highest and lowest value are 6.2 and 3.7%, respectively. Since variation in the other variables such as number of clutches, number of eggs, and egg size is usually much larger, assuming a constant energy density would provide reasonably accurate comparative estimates of the energy incorporated into egg production in most cases. Certainly the number of egg sacs, number of eggs, and egg size can be counted and measured with ease and accuracy thus permitting more extensive studies of the energetics of reproductive output than would otherwise be practical.

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A NEW SPECIES OF *LINOTHELE* FROM COLOMBIA (ARANEAE, MYGALOMORPHAE, DIPLURIDAE)

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ABSTRACT

Linothele megatheloides is newly described from Colombia. It differs from other species of *Linothele* by the larger size, very long posterior lateral spinnerets and scopulate tarsi of females.

INTRODUCTION

Linothele is one of three diplurid genera that build conspicuous webs in South and Central America (see Paz S. 1988); the others are *Diplura*, with which it was long confused (see Raven 1985), and *Ischnothele*. Spiders of these genera build expansive sheet webs leading to a funnel in overhangs of banks and shelters formed by tree buttresses (Coyle 1986). The web includes numerous large corridors through which the spider runs while holding the very long spinnerets high above the abdomen. Paz S. (1988) has discussed the behavior and ecological aspects of this new species. All measurements are in millimeters and abbreviations are standard for the Araneae.

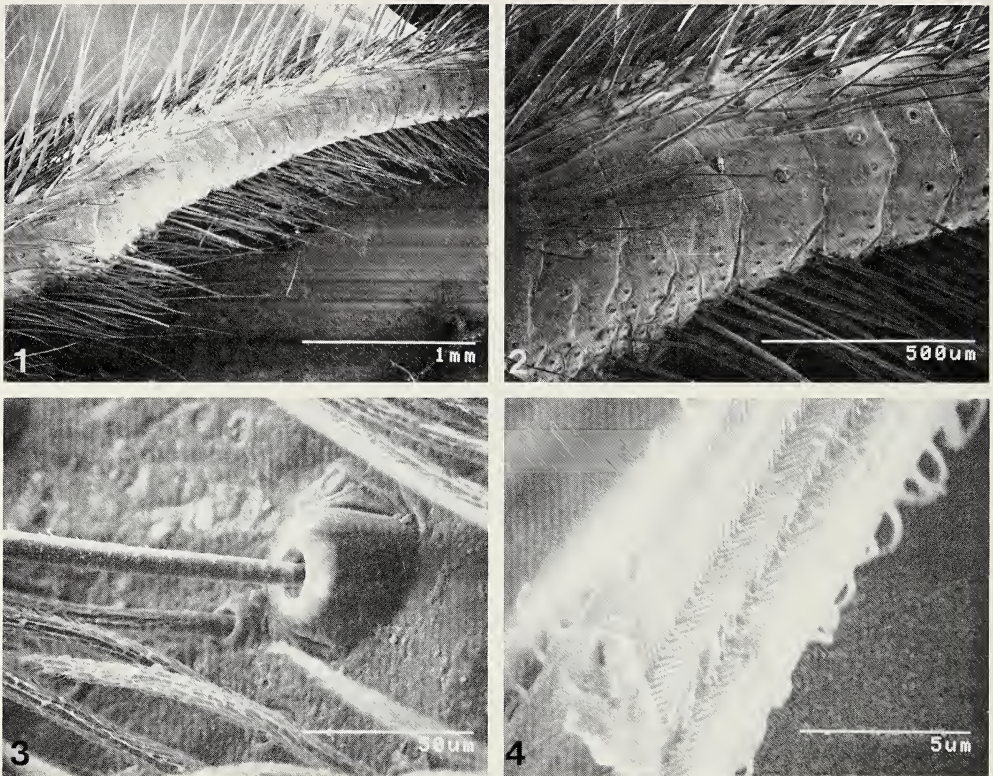
***Linothele megatheloides*, new species**

Figs. 1-12

Types.—Holotype male, paratype female from Tutunendo, Choco, Colombia, (27 July 1983; N. Paz S.), deposited in the American Museum of Natural History.

Etymology.—The specific epithet refers to the very long posterior lateral spinnerets.

Diagnosis.—*L. megatheloides* differs from *L. macrothelifera* Strand, 1908 (type in Senckenberg Museum, Frankfurt, examined), which also has long spinnerets, in the much larger size, very long spinnerets (Fig. 9), pseudosegmented apical article of posterior lateral spinnerets, and the presence of some scopulae on tarsi of females.



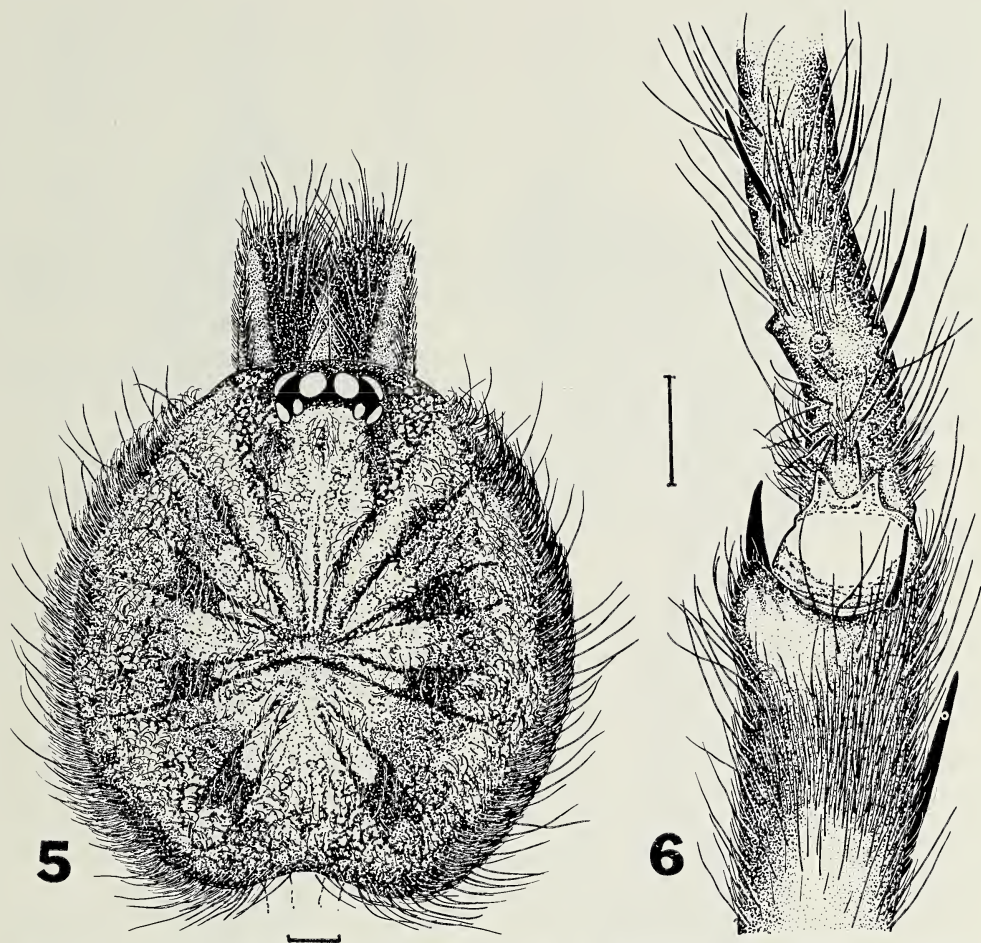
Figures 1-4.—*Linothele megatheloides*, female. Scanning electron micrographs: 1, 2, tarsus I (shaved) showing pseudosegmentations; 3, cuticle and trichobothrial base with shallow corrugations; 4, ventral "scopula" hair.

Description.—*Holotype male*: (Figs. 5-8, 12). Total length, including chelicerae, 33. Carapace red brown, striae marked by black reticulations along edges; caput brown with donut-shaped darkened ring medially; chelicerae, and legs red brown. Dorsum of abdomen brown with two lighter colored longitudinal bands, venter brown.

Carapace 10.83 long, 9.83 wide; with fine black hairs and bushy band of black hairs on margins. Foveal bristles absent; one long bristle between PME, four long on clypeal edge; 4 long between PME; no anteromedial bristles; few in striae; striae distinct. Fovea short, recurved; clypeus absent.

Eight eyes on tubercle occupying about 0.50 of front width. Ratio of eyes, anterior lateral: anterior median: posterior lateral: posterior median, 34:33:25:18. Anterior row slightly procurved; medians separated by 0.2 of their diameter, 0.2 from laterals. Posterior row recurved, medians separated by 1.6 times AME diameter, 0.2 from laterals. Median ocular quadrangle wider than long (74/46), narrower in front (61/74). Lateral eyes of each side separated by 0.2 of AME diameter.

Sternum 4.08 long, 4.06 wide; covered with long erect black bristles mixed with fine hairs; sigilla oval to subcircular, marginal. Labium 1.44 long, 2.00 wide, with no cuspules. Palpal coxae 3.20 long behind, 2.96 long in front, 1.36 wide, with 28-30 cuspules (not on mound) on inner angle; anterior lobe indistinct. Chelicerae small, slender, with dorsal band of fine brown hair and few black bristles;



Figures 5, 6.—*Linothele megatheloides*, holotype male: 5, carapace and chelicerae, dorsal view; 6, tibia and metatarsus I, proventral view. Scale lines = 1 mm.

promargin with about 5 large and 6 small and 2 very small teeth, basomesally with 2 small teeth.

Leg formula 4123. Spination (no spines on tarsi): leg I, femur p3d4r3, patella p1, tibia p2r2v3 + megaspine, metatarsus plv5; leg II, femur p3d3r3, patella p1, tibia plrlv4, metatarsus plv8; leg III, femur p3d3r4, patella plrl, tibia p3r3v6, metatarsus p5r4v8; leg IV, femur p3d4r5, patella p1, tibia p2r3v6, metatarsus p5dlr3v9. Scopulae: tarsi I, II, thin for distal three quarters; tarsi III scopulate for distal half, entire; tarsi IV scopulate, divided by setae for distal one-fifth. All leg tarsi curved, pseudosegmented. Tibia I distally with retrolateral mound bearing megaspine (Fig. 6), ventral metatarsus I with rounded thumb proximally with conical process above it on mid-lateral face. Paired tarsal claws with two rows of teeth, one short distal of about 4 teeth on inner edges, about 7 proximally on outer edges; third claw bare. Trichobothria: 20-30 in slightly irregular row on tarsi; 30-40 in curving line on metatarsi; about 11 for half of tibial length in each of two rows.

	I	II	III	IV	Palp
Femur	12.85	12.54	11.00	14.05	7.40
Patella	4.95	4.75	4.15	4.63	3.40
Tibia	11.11	10.63	9.86	12.82	6.96
Metatarsus	12.96	13.05	14.15	18.80	—
Tarsus	8.76	9.30	8.35	9.60	2.40
Total	50.63	50.27	47.51	59.90	20.16

Palp (Fig. 8) with long slender tibia; cymbium short rounded; bulb pyriform with small subtegulum; embolus broad with scooped tip. Spines, femur p1d4r1, patella 0, tibia p2v2.

Abdomen 13.30 long, 5.35 wide. Three-segmented posterior lateral spinnerets with basal, median, apical segments 6.83, 7.33, 12.83 long, respectively. Posterior median spinnerets 2.56 long, 0.24 wide, 0.96 apart.

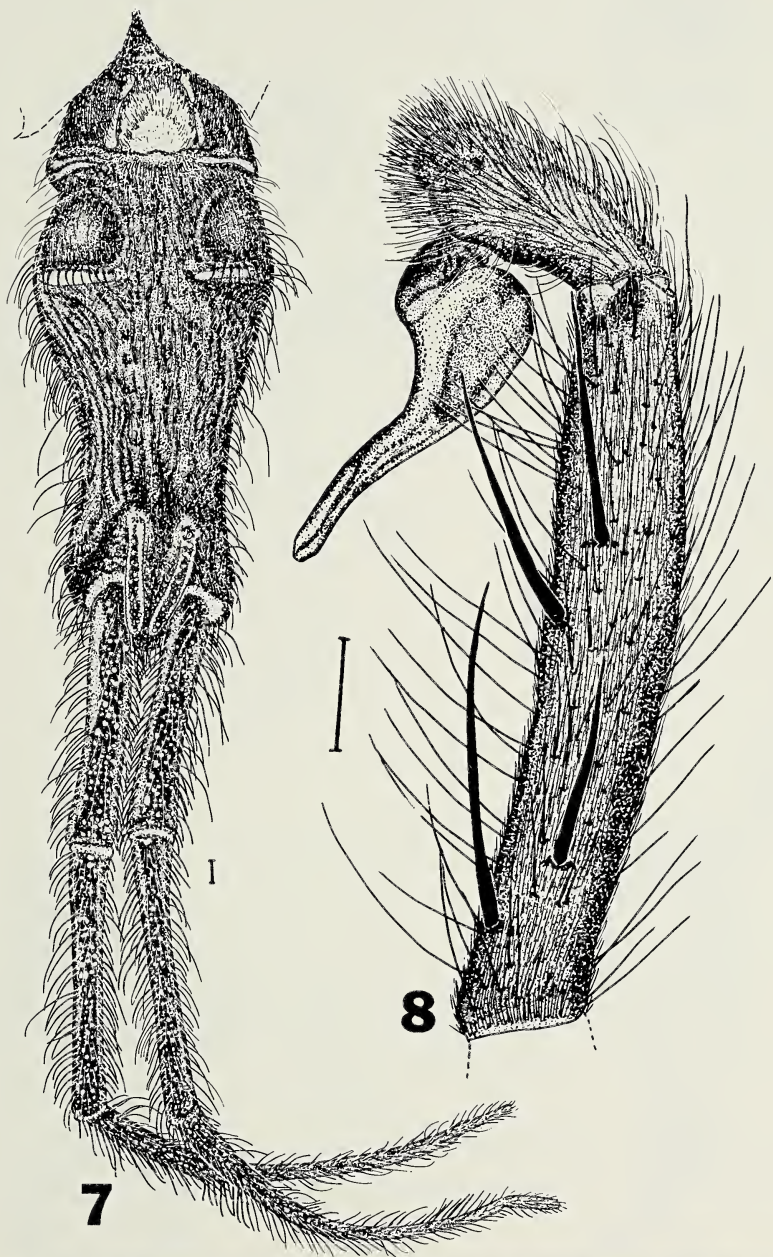
Paratype female: (Figs. 9-11). Total length, including chelicerae, 43. Carapace orange brown with brown mottling on caput and interstrial ridges; chelicerae and legs red brown. Dorsum of abdomen brown with medial pallid area, venter brown.

Carapace 13.17 long, 12.33 wide; with golden brown hairs forming bush on lateral margins and along striae edges; setation less dense centrally. Foveal bristles absent. Fovea short recurved open; clypeus narrow, distinct; caput low; striae deep, distinct; seven thick bristles on clypeal edge.

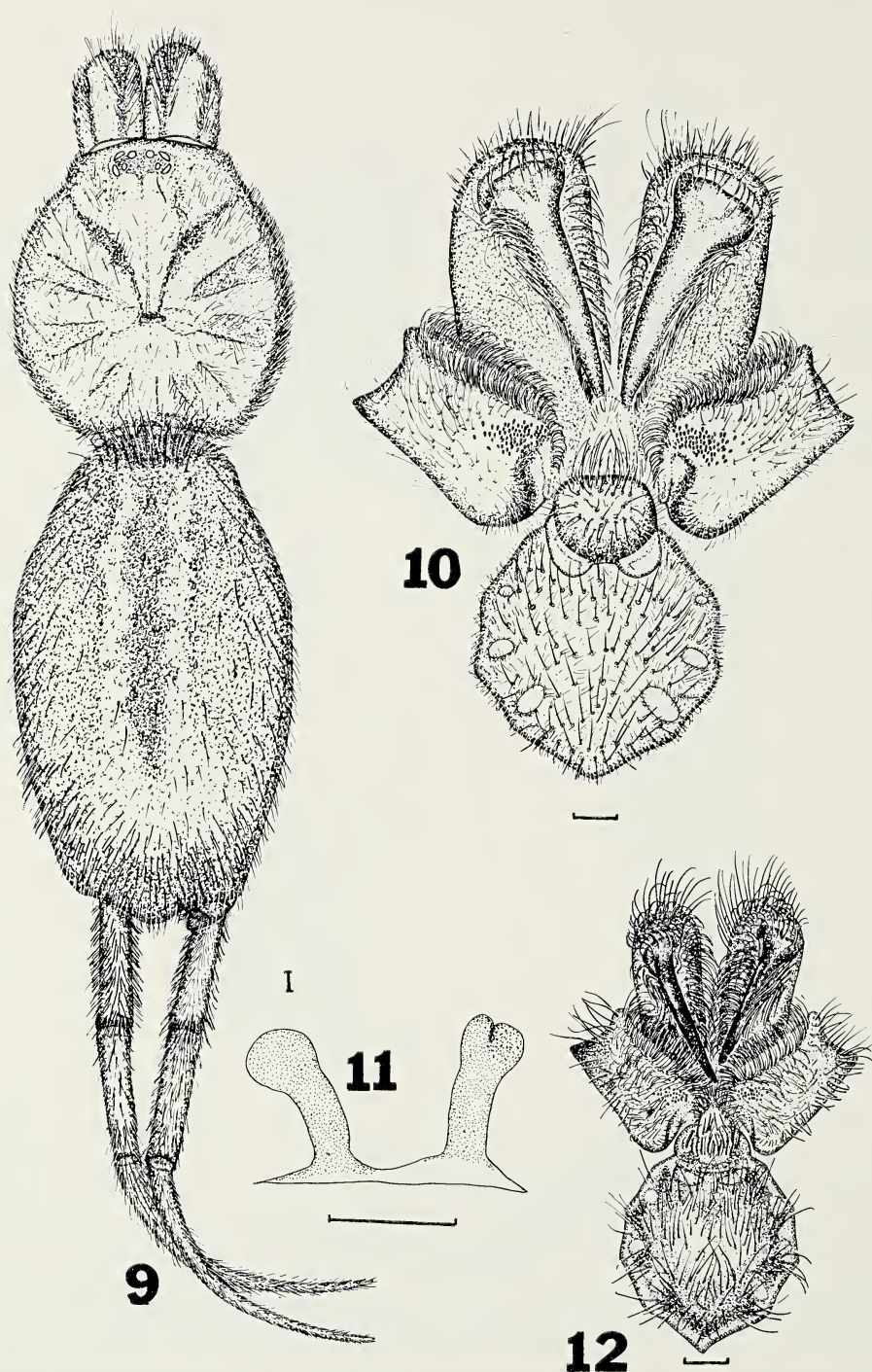
Eight eyes on tubercle occupying about 0.39 of front width. Ratio of eyes, anterior lateral: anterior median: posterior lateral: posterior median, 18:15:16:12. Anterior row straight; medians separated by 0.6 of their diameter, 0.2 from laterals. Posterior row recurved, medians separated by twice their diameter, 0.1 from laterals. Median ocular quadrangle wider than long (47/25), narrower in front (35/47). Lateral eyes of each side separated by 0.2 of AME diameter.

Sternum 6.08 long, 5.60 wide; length of posterior, 1.00, middle, 0.64, sigilla, respectively, all oval to sub-oval, marginal. Labium 1.92 long, 2.40 wide, with no cuspules. Palpal coxae 5.04 long behind, 4.24 long in front, 2.40 wide, with about 60 cuspules (not on mound) on inner angle; anterior lobe indistinct with well-developed serrula. Chelicerae short, rounded, geniculate, with long brown bristles between golden brown pile; promargin with about 5 large and 7 smaller teeth, basomesally with 30-40 granules and 7 small teeth.

Leg formula 4123. Numerous bushy hairs on pro- and retrolateral femora; peacock blue hairs on all femora, patellae, and tibiae. Spination (no spines on tarsi): leg I, femur p3d2r1, patella p1, tibia p2v4, metatarsus v6; leg II, femur p4d3r1, patella p1, tibia p2v4, metatarsus p1v7; leg III, femur p3d3r3, patella p1r1, tibia p2r2v6, metatarsus p5r3v8; leg IV, femur p3d3r4, patella p1r1, tibia p2r1v6, metatarsus p5r5v8. Scopulae: tarsus I, thin for full length, divided by two almost straight lines of setae; tarsus II, as for I but distally setal lines becoming irregular forming about 4 rows; tarsus III and IV, as for II, but divided by 2-3 rows on III, and by 8-10 rows of setae with scopula reduced to two narrow bands on IV. Scopula hairs with longitudinal grooves with common herring-bone corrugations (Fig. 4); few fimbriations present. All tarsi pseudosegmented (Figs. 1, 2), with transverse fissures almost circling segment; ventrally fissures divide forming separate diamond-shaped plates. Paired tarsal claws with two rows, one short distal of about 4 teeth on inner edges, about 7 proximally on outer edges;



Figures 7, 8.—*Linothele megatheloides*, holotype male: 7, holotype male, abdomen and spinnerets, ventral view; 8, palpal tibia, cymbium and bulb, retrolateral view. Scale lines = 1 mm.



Figures 9-12.—*Linothele megatheloides*: 9-11, female paratype; 9, carapace, chelicerae, abdomen, and spinnerets, dorsal view; 10, sternum, maxillae, labium, and chelicerae, ventral view; 11, spermathecae, ventral view; 12, holotype male, sternum, maxillae, labium, and chelicerae, ventral view. All scale lines = 1 mm.

third claw bare. Trichobothria similar to male; base of bothrium with shallow indistinct corrugations near aperture (Fig. 3). Cuticle almost smooth.

	I	II	III	IV	Palp
Femur	13.94	14.15	12.76	16.35	9.01
Patella	6.95	6.10	5.50	6.00	4.98
Tibia	12.50	11.35	10.45	13.62	7.76
Metatarsus	11.90	12.10	13.24	17.78	—
Tarsus	7.05	7.17	7.40	8.80	6.91
Total	52.34	50.87	49.35	62.55	28.66

Palpal spines, femur p1d4r1, patella p3, tibia p2v6, tarsus v2. Claw with six very short teeth on short diagonal row.

Abdomen 22.17 long, 12.50 wide. Three-segmented posterior lateral spinnerets with basal, median, and apical segments 7.83, 7.50, 15.00 long, respectively. Posterior median spinnerets represented only by scars. Spermathecae two, each with long lobe apically enlarged with a shallow apical invagination.

Material Examined.—The holotype plus 1 male, 2 females, 2 penultimate males, between kilometers 178-134, via Quibdo, Medellin, at an altitude of 85 m, N. Paz S., 20 Feb. 1983, deposited in the American Museum of Natural History, New York.

Remarks.—The pseudosegmented tarsi (Figs. 1, 2; see Raven 1985 for explanation of wider occurrence) are extremely flexible. They are considered the most apomorphic state of leg tarsi in mygalomorphs; other states being cracked tarsi (usually only one or few transverse fissures), pallid cuticle that is indicative of a weakness, and normal tarsi. In *L. megatheloides*, closer study of the pseudosegmentation (Fig. 2) shows that the “cracking clay” affect may be quite regular laterally.

Associated with the pseudosegmented tarsi (and diagnostic of the Diplurinae) are what appear to be scopulae. The hairs resemble a scopula because they are short, straight, erect, and on the ventral surface of the tarsi. The hairs show the same canaliculi or fluting as that seen on the leg setae (dorsal) and spines of many mygalomorphs, and have very few fimbriations which would increase surface area. In contrast, leg scopulae of theraphosids are dense pads of highly fimbriated setae. It is thus likely that the term “scopula” needs to be redefined. Further study is needed to test the hypothesis that the leg scopulae of the Crassitarsae (Raven 1985) are homologous.

In most Tuberculotae, the bothrial bases are corrugiform. In some cases, the corrugations cover the base (e.g., the six-eyed diplurid *Masteria*; Raven 1979, fig. 21). However, in *Linothele megatheloides*, the corrugations are very shallow and confined to the upper portion of the base.

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THE EFFECT OF TIME AND TEMPERATURE ON DISTURBANCE BEHAVIORS SHOWN BY THE ORB-WEAVING SPIDER *ULOBORUS GLOMOSUS* (ULOBORIDAE)

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ABSTRACT

When disturbed, *Uloborus glomosus* either remain in position at the hub of their orb-webs, jump from the web, move to the edge of the web, or shake the web. The time of day influences which of these behaviors is expressed. Spiders tend to jump in the afternoon and the evening but not in the morning. In the morning they tend to move to the edge of the web or remain in position. The tendency to shake the web is approximately the same throughout the day. Ambient temperature appears not to be the principal factor explaining the differences in jumping, moving to the edge, and remaining in position. Historical differences in the activity patterns of various spider predators may have influenced the time-related expression of disturbance behavioral patterns.

INTRODUCTION

Many orb-weaving spiders show predictable responses when disturbed. Some run to a retreat or to surrounding vegetation, others move to the edge of the web, others shake the web and others jump from the web (Pekham and Pekham 1887; Levi 1968; Marples 1969; Eberhard 1970, 1973; Robinson and Robinson 1970; Robinson 1978; Ewer 1972; Edmunds 1974; Tolbert 1975; Levi 1977; Hoffmaster 1982; Cushing and Opell in press). These behaviors are thought to be predator avoidance strategies. The jumping and shaking responses have been cited as responses to a variety of predators including both spider-hunting wasps and salticid spiders (Richards and Hamm 1939; Eberhard 1970; Coville 1976; Hoffmaster 1982; Cushing and Opell in press).

When the spider *Uloborus glomosus* (Walckenaer) (Uloboridae) is disturbed while resting beneath the hub of its horizontal orb-web, it may show one of four responses: jumping from the web, shaking the web, moving to the edge of the web, or remaining in position (Cushing and Opell in press). Many factors, including time of day, evidently influence the expression of the behaviors. The objectives of this study are to determine how time of day influences the disturbance behaviors shown by these spiders and if temperature mediates these behavioral patterns.

METHODS

Forty-nine adult female *Uloborus glomosus* were collected from shrubbery at various locations on the V. P. I. and S. U. campus (Blacksburg). When collected no spiders had eggsacs, although many subsequently produced eggsacs, a factor not considered in the analyses. Twenty-five spiders were collected in mid-July, 1987 and assigned to Group I. Others collected in late July were in Group II. All spiders were maintained in an outdoor study enclosure in a wooded area of Blacksburg.

Spiders in Group I were marked for identification by applying small dots of green and red enamel paint to their dorsal abdominal surfaces. The dots were observed by holding a long-handled dental mirror beneath a spider on its orb web. Group I spiders were established on six frames, each providing a vertical series of 25 wooden dowel rods spaced 12 cm apart. Each rod was 8 mm in diameter and 50 cm long. Spiders chose their own web attachment sites and were maintained at a density of one to four spiders per frame. Frames were kept in a $3 \times 3 \times 3$ m screened enclosure to prevent dispersal away from the study area. Group II spiders were kept in $31 \times 16.5 \times 9$ cm plastic shoeboxes covered with mosquito netting and placed under a plastic roof just outside the screened enclosure housing Group I spiders. We began testing Group I on 13 July, and Group II 7 days later. Group I spiders were removed and the experiment terminated after 19 days of testing. Group II spiders were tested for 36 days.

As a disturbance stimulus we dropped water on the venter of each spider from a Pasteur pipette with an average tip diameter of 1.20 mm held 1 cm above the spider. The water was kept in the enclosure to maintain it at ambient temperature. This stimulus was suggested by W. G. Eberhard (pers. comm.) as it is more easily standardized than touching the spider with a probe. A water drop was considered to approximate the sudden ventral contact by an attacking predator such as a wasp or a hunting spider. Since *U. glomosus* does not respond to the visual or vibratory stimuli produced by a tethered wasp held directly above the spider (Cushing and Opell in press), visual and vibratory stimuli were considered inappropriate disturbance stimuli. After stimulating a spider, we recorded its response to this disturbance as either: jumping out of the web, moving to the edge of the web, remaining in position, or shaking the web. Preliminary observations showed that the spiders responded similarly to a water drop as to contact by a small probe.

Temperature was recorded at the time observations were begun. It took approximately 30 minutes to test all of the spiders' responses. For both groups, we tested all spiders in the morning (0800-1000 hours) of day 1 of the tests and recorded their behaviors. On day 2, we tested all the spiders in the afternoon (1200-1400 hours) and on day 3 we tested them in the evening (1600-1800 hours). These times corresponded to the times used by Cushing and Opell (in press). Spiders were not disturbed on day 4 to ensure 24 hours between tests. This 24 hour testing sequence was a cautionary measure chosen to diminish any degeneration of the behaviors that might result from too frequently disturbing the spiders. On day 5, the 3-day cycle, hereafter referred to as a block, was repeated. Group I spiders were run for 5 blocks (15 days of actual testing) and Group II spiders for 9 blocks (27 days of actual testing).

Table 1.—The frequencies of each behavior during the morning, afternoon and evening. Total number of observations is 862. *=Two spiders died before the final evening observations were recorded.

Response	Time of day			Total
	Morning	Afternoon	Evening	
Jumped from web	116	172	169	457
Moved to edge	26	11	13	50
Remained in position	70	38	39	147
Shook web	76	67	65	208
Total	288	288	286*	862

If a spider died or disappeared before half of the observations were completed, all the previous observations for that individual were eliminated from the data set. This ensured that each spider in Group I and in Group II contributed an approximately equal sequence of observations to the data set. Consequently, a spider from Group I had to survive through block 3 for its behaviors to be included in the analyses and one from Group II had to survive through block 5. Observations for 22 Group I and for 21 Group II spiders were used in the final analyses.

To supplement their diet of small insects that passed into the enclosure, we fed all spiders by blowing several fruit flies (*Drosophila* sp.) into their webs, either after testing in the evening of the three-day cycle or on the fourth (non-test) day. Group II spiders relied solely on this source of food.

To determine the validity of pooling the responses of all 43 spiders, we conducted a Replicated Goodness-of-Fit Test for heterogeneity (Sokal and Rohlf 1981), comparing the pooled responses of Group I spiders with the pooled responses of Group II spiders. To determine the effect of the variable Time on the responses of these spiders, we pooled the observations for each of the behavioral categories made during each of the three time periods across all 43 spiders for a total of 882 observations (Table 1). We conducted a log-linear analysis to determine if the variables Time and Response are associated and, if so, to establish the patterns of behavioral switching that occurred (Bishop et al. 1975; Fienberg 1987).

To assess the magnitude of the interactions between each of the three Time categories with each of the four Response categories, we calculated the ratios of the log-linear parameter estimates to the standard errors for the log-linear model with the two-way interaction term between Time and Response. These ratios are somewhat analogous to cell chi-square values. The greater the ratio term, the greater the effect of those categories on the association between Time and Response. As the parameter estimates are calculated according to the assumption of normality, ratio terms greater than /1.96/ correspond to a significance level less than 0.05 in a Z-table and indicate category interactions that contribute most to the association between Time and Response. Positive ratios indicate a positive interaction between the categories; negative ratios indicate a negative interaction (Kennedy 1983).

To determine the effect of Temperature on the behaviors, we conducted a discriminant analysis, defining Temperature as the independent continuous variable and Response as the classification variable.

Table 2. Ratio terms (Z-values) for the Time \times Response association. * = $P < 0.05$.

Response	Time		
	Morning	Afternoon	Evening
Jumped from web	-5.541*	2.919*	2.333*
Moved to edge	2.233*	-1.290	-0.581
Remained in position	2.107*	-0.867	-0.972
Shook web	-1.023	0.800	0.139

RESULTS

Association between Time and Response.—The test for heterogeneity between Groups I and II indicated that they were homogeneous ($G^2 = 1.1078$, $P > 0.5$). Therefore, we pooled responses for all 43 spiders. Over the entire testing period, spiders jumped from the web 53% of the time, moved to the edge 6% of the time, remained in position 17% of the time, and shook the web 24% of the time (Table 1).

The two-way log-linear analysis comparing the interaction between the Time and Response variables indicated that spider response is influenced by the time of day ($G^2 = 34.947$, $P < 0.001$). The magnitudes of the interactions between each of the Time categories with each of the Response categories is presented in Table 2. In the morning, spiders did not tend to jump from the web in response to the disturbance but did tend to either move to the edge of the web or remain in position. Spiders tended to jump from the web in the afternoon and the evening. They showed no time-related preference for the shaking behavior although shaking the web was the second most frequent response (Table 1).

Effect of Temperature on the behaviors.—The mean temperature during the morning tests was 20.2°C (SD = 3.05); the mean during the afternoon tests was 28.2°C (SD = 3.01); and the mean during the evening tests was 26.8°C (SD = 3.07).

To calculate the discriminant function, the within-group covariance matrix rather than the pooled covariance matrix was used because the within-group covariance matrix for the Response variable was not homogeneous ($\chi^2 = 0.004$, $P < 0.05$, Kleinbaum and Kupper 1978). According to the discriminant analysis, temperature is not a good predictor of the disturbance behaviors (Table 3).

DISCUSSION

This study supports Cushing and Opell's (in press) finding that *Uloborus glomosus* responds differently to disturbance at different times of the day. It also indicates that ambient temperature may not be the principal factor explaining these differences. Temperature correctly predicted whether a spider moved, shook, or remained in position less than 42% of the time; the jumping response was correctly predicted 66% of the time. The jumping response appears to be an energetically expensive behavior (Cushing and Opell in press) and, therefore, may be enhanced by higher temperatures.

Jumping from the web is effective against aerial hunters such as spider-hunting wasps and hummingbirds (Eberhard 1970; Coville 1976; Hoffmaster 1982;

Table 3.—Observations (Total 862) correctly and incorrectly assigned by a discriminant analysis to each of the Response categories using Temperature as a predictor.

Response	Freq.	% Correctly assigned	% Incorrectly assigned to:			
			Jumped	Moved	Remained	Shook
Jumped from web	457	66.1	—	1.8	19.9	12.3
Moved to edge	50	12.0	40.0	—	42.0	6.1
Remained in position	147	41.5	28.6	13.6	—	16.3
Shook web	208	17.3	45.7	1.9	35.1	—

Cushing and Opell in press). Wasps are not very successful at stinging spiders hanging on threads beneath orb-webs and rarely pursue spiders after they have jumped unless they have landed on a solid substrate (Eberhard 1970). The same is probably true for hummingbirds, one of the more important avian predators of spiders. These birds supplement their nectar diet with protein from spiders (including orb-weavers) and insects (Pyke 1980; Johnsgard 1983).

Jumping behavior does not appear to be effective against ambulatory predators such as salticid spiders. Robinson and Valerio (1977) noted that araneids that jumped from their webs after being attacked by salticids could not displace the jumping spider. When a spider jumps from its web, it also risks losing a productive web site if its dragline breaks or becomes entangled in surrounding vegetation, falling into the web of a neighboring spider, or becoming prey of an ambulatory predator on the substrate to which it falls. Therefore, if the stimulus is not immediately threatening an alternate avoidance strategy such as shaking the web may be advantageous. This behavior may dislodge an ambulatory predator (i.e., a salticid spider) from both the orb-spider and the web plane (Robinson and Valerio 1977; Hoffmaster 1982).

If it is true that jumping from the web is most effective against aerial predators and shaking the web against ambulatory predators, then the expression of these behaviors at particular times of day may have been selected by differences in the activity patterns of these predators. Hummingbirds are primarily nectar feeders. Nectar flows most abundantly from one to two hours before hummingbirds become active (about 0430 hours) until around 1830 hours when hummingbirds cease activity (Cruden et al. 1983). Hummingbirds tend to hunt insects and spiders only casually in the morning, spending most of their time feeding on nectar. They more actively hunt arthropods as the day progresses (after nectar production has dropped off) (Stiles and Wolf 1979; Gill pers. comm.).

Adult spider-hunting wasps of the families Sphecidae and Pompilidae are also primarily nectar feeders only occasionally eating the spiders they hunt (Evans and Eberhard 1970). Coville (1987) states that these wasps are active from one to three hours after sunrise to one to three hours before sunset. Although their daily activity cycles have not been described, it is probable that they also spend the early morning hours foraging for nectar. They seem to build their nests and hunt for spiders most actively between 1100 hours and 1830 hours (Bristowe 1948; Cushing 1988).

The activity patterns of these aerial predators may explain the tendency of *U. glomosus* to jump in the afternoon (1200-1400 hours) and the evening (1600-1800

hours) but not in the morning (0800-1000 hours). If this explanation is correct, the jumping response should be as infrequent late in the day (i.e., from 1800-2000 hours) as in the morning. Spiders that jump in the afternoon and the evening but not in the morning must switch to some other behavior in the early hours. This study suggests that these spiders move to the edge of the web or remain in position when disturbed. Both of these behaviors are energetically and strategically inexpensive, but probably not very effective if the stimulus is an actual ambulatory (or aerial) predator.

Shaking behavior is the second most frequent behavior and occurs at equal frequency regardless of time of day or temperature. This may also be related to the activity pattern of the main predator group to which it is directed, namely ambulatory predators. Salticid spiders are an important ambulatory predator of orb-weaving spiders, especially in the tropics (Bristowe 1941; Enders 1974, 1975; Robinson and Valerio 1977; Edwards pers. comm.). Their activity patterns have been described as beginning as early as 0700 hours and ending as late as 1900 hours (Anderson 1970; Abraham 1983), although Gardner (1965) and Edwards (pers. comm.) have observed salticids hunting most actively between 1000 hours and 1600 hours. Because these ambulatory predators are active throughout the day, the shaking behavior should also be shown throughout the day, as this study shows it to be.

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TWO NEW SPECIES OF *ISCHNOTHELE* FUNNELWEB SPIDERS (ARANEAE, MYGALOMORPHAE, DIPLURIDAE) FROM JAMAICA

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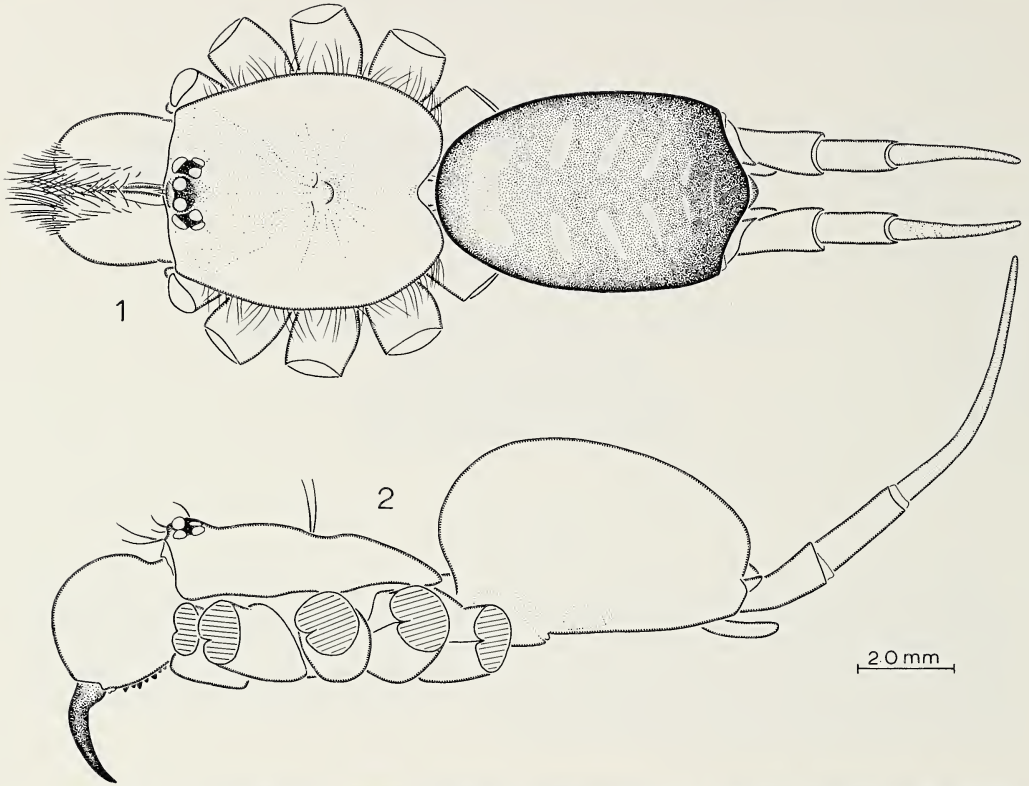
ABSTRACT

Based upon an analysis of patterns of variation in morphology, pigmentation, habitat, and *Mysmenopsis* kleptoparasites, two new species of *Ischnothele* from Jamaica (*I. reggae* and *I. xera*) are described. These allopatric sister species appear to have cospeciated with their respective *Mysmenopsis* kleptoparasite species, also each other's closest relatives. The rate of divergent evolution of the two kleptoparasite populations appears to be greater than that of the host populations, in part, we suggest, because of the kleptoparasites' shorter generation time.

INTRODUCTION

This study is part of the first author's revisionary study of the ischnotheline funnelweb spiders, tropical diplurids with two rows of cheliceral teeth, an elongate terminal cymbial apophysis, and maxillary (but not labial) cuspules. The genus *Ischnothele* (Figs. 1, 2) is distributed throughout much of the American tropics and differs from the other two (Old World) ischnotheline genera (*Thelechoris* and *Lathrothele*) by the presence of spines on the male tibia I apophysis (Figs. 12-17), by the presence of an opposing protuberance on the male metatarsus I (Figs. 12-17), and by a reasonably clear demarcation between the bulb and embolus (Figs. 22, 23).

The unpublished occurrence of *Ischnothele* on Jamaica came to light during an examination of museum collections and prompted the first author to make a four-day visit to that island in early April of 1988 during a collecting trip to the American tropics. Collecting in Jamaica was limited to several areas in the southeastern part of the island (the source of 95% of previously collected specimens) and revealed marked geographic variation in the habitat, kleptoparasites, pigmentation, and morphology of these *Ischnothele* populations. Although more careful searching in this and other parts of Jamaica for additional and larger population samples will be needed to rigorously test hypotheses about *Ischnothele* species limits, we believe that we currently have sufficient data to postulate that there are two species of *Ischnothele* on Jamaica, and we hope that the presentation of such information will stimulate and guide future research. Moreover, our findings provide the first clear evidence for the kind of host-kleptoparasite cospeciation process which may be a key factor in the evolution of



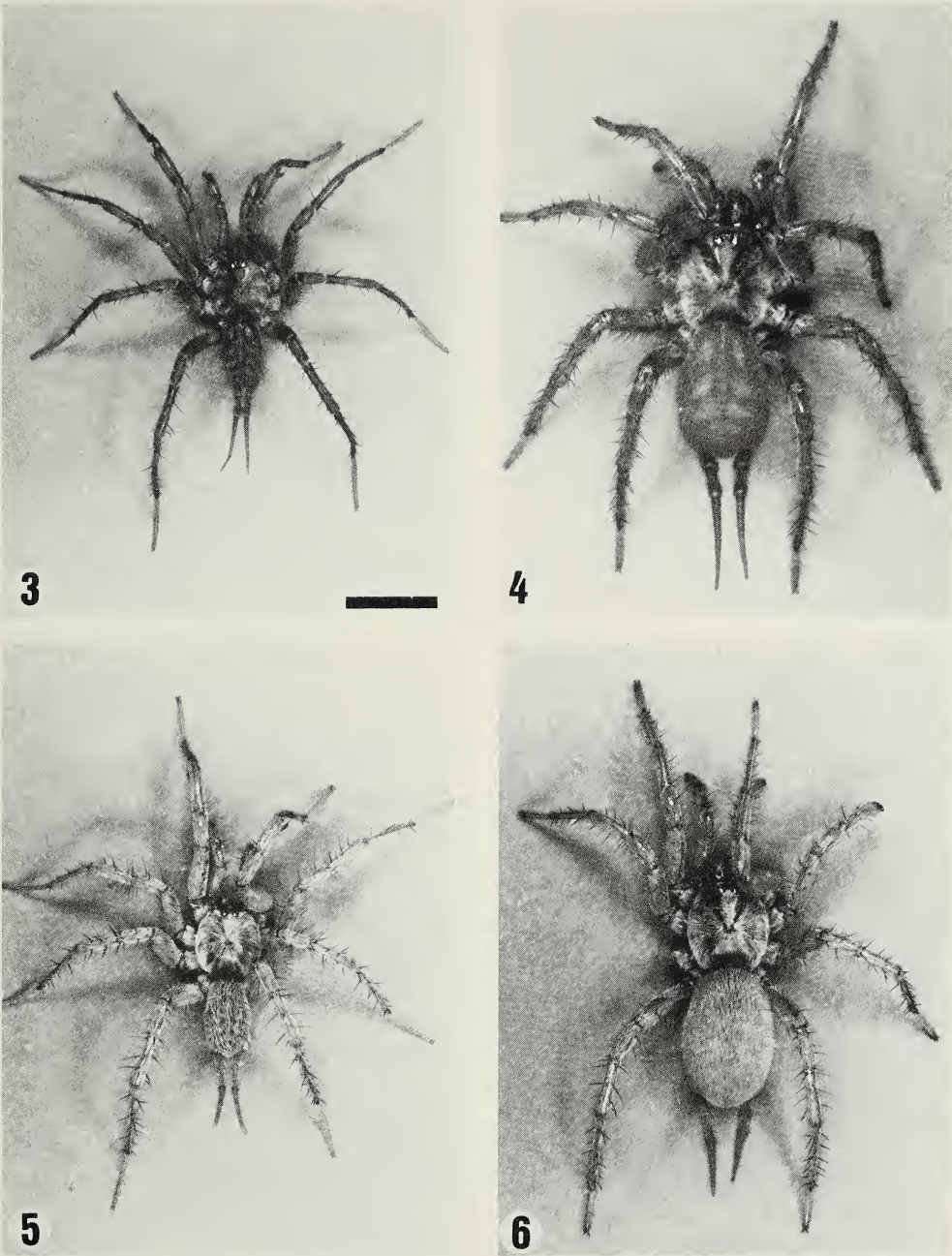
Figures 1, 2.—*Ischnothele reggae* paratype, female body; 1, dorsal, showing abdominal pigmentation and bristles on chelicerae and carapace; 2, lateral.

the mysmenid genus *Mysmenopsis* (Platnick and Shadab 1978; Coyle and Meigs 1989), many species of which are kleptoparasites of diplurid spiders.

These two species of *Ischnothele* are endemic to Jamaica and are clearly each other's closest relatives. Of the several probable synapomorphies linking these species, two are especially distinctive: (1) spermathecae short and stalkless (or with a very short, broad vestigial stalk), and (2) embolus serrated. Two synapomorphies support the hypothesis that this species pair is most closely related to endemic species from Cuba (*Ischnothele longicauda* Franganillo) and Hispaniola: (1) ventral surface of male metatarsus I with distal keel, and (2) embolus short. A more complete phylogenetic analysis of all ischnotheline taxa will be presented in the forthcoming revision.

METHODS

The quantitative characters used in this study are abbreviated and defined as follows: MC, number of cuspsules on ventral surface of maxilla; ITSP and ITSR, number of spines on prolateral and retrolateral surfaces of male tarsus I, respectively; TAS, number of spines on male tibial mating apophysis; CSP and CSR, number of enciform spines on prolateral and retrolateral surfaces of male cymbial apophysis, respectively; CTP and CTR, number of cheliceral teeth in prolateral and retrolateral rows, respectively; CDP and CDR, number of



Figures 3-6.—Photos of living specimens of Jamaican *Ischnothele* species, dorsal view; 3, 4, *I. reggae*; 3, male holotype; 4, female paratype; 5, 6, *I. xera*; 5, male holotype; 6, female paratype. Scale bar = 5 mm.

cheliceral denticles adjacent to prolateral and retrolateral rows of teeth, respectively; PTarS, number of spines on female palpal tarsus; ITarS, number of spines on female tarsus I; CS, length of longest seta protruding from male carapace edge above coxa III; CL, carapace length; CW, carapace width; AMD, transverse diameter of left anterior median eye pupil; AMS, minimum distance

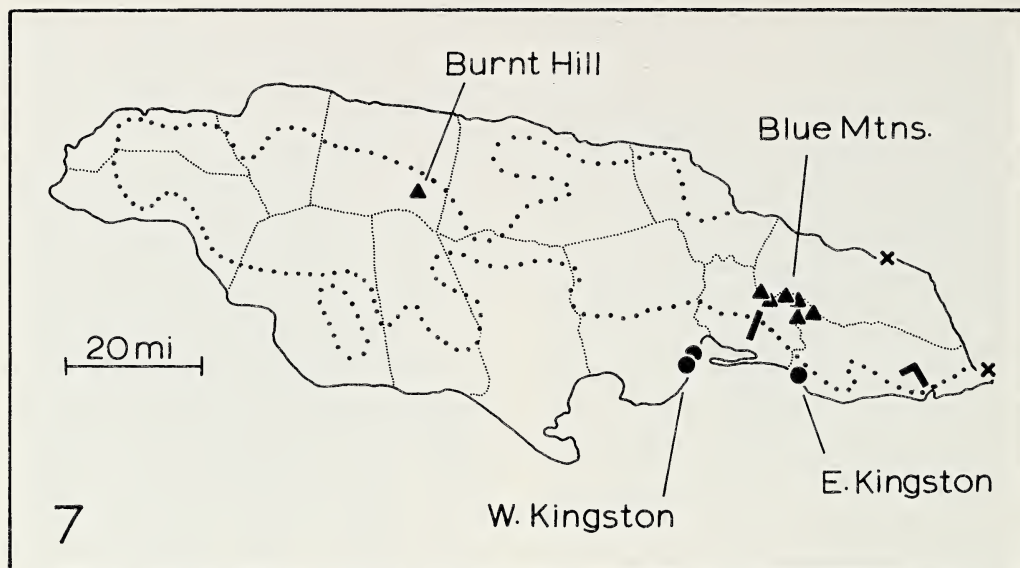


Figure 7.—Distribution of Jamaican *Ischnothele* species. Triangles designate collection localities for *I. reggae*, circles for *I. xera*, X's for juveniles only. Black bars designate areas where first author searched unsuccessfully for *Ischnothele*. Dotted line encloses area receiving over 75 inches of rainfall per year.

between anterior median eye pupils; OQW, ocular quadrangle width; SL, sternum length; SW, sternum width; IFL, ITL, IML, and ITarL, lengths of leg I femur, tibia, metatarsus, and tarsus, respectively; ITT, maximum diameter of male tibia I in retrolateral view along line perpendicular to ITL; MKP, distance along IML line from proximal end of male metatarsus I to the intersection with perpendicular line passing through the prolateral keel apex; TAL, distance from disto-dorsal angle of male tibia I apophysis to base of apophysis in retrolateral view (Fig. 15); TAW, midpoint diameter of male tibia I apophysis in retrolateral view (Fig. 15); PFL and PTL, lengths of male palpal femur and tibia, respectively; PTT, maximum diameter of male palpal tibia in retrolateral view along line perpendicular to PTL; CYL, length of male cymbium (including apophysis) in prolateral view; CYAL, length of male cymbial apophysis from apex of prolateral cymbial lobe to tip of apophysis along line parallel to CYL; PL, distance from tip of embolus to most distant edge of palpal bulb (Fig. 23); PD, maximum diameter of palpal bulb (Fig. 23); ML, distance from proximal-most maxillary cuspule to tip of endite along line parallel to longitudinal axis of maxilla with ventral surface of maxilla in horizontal plane; CFL, distance along ML from proximal-most cuspule to perpendicular line that intersects distal-most cuspule; LSL1, LSL2, and LSL3, lengths of posterior lateral spinneret articles (basal, middle, and terminal article, respectively) measured along midventral line.

All appendage character states were recorded from the left appendage (unless missing, damaged, or not fully regenerated) except for ITSP, ITSr, TAS, CSP, and CSR, which were recorded from both appendages. All carapace and eye measurements were performed in dorsal view with the lateral borders of the carapace in the horizontal plane. The length of each leg article and of the palpal femur and tibia was measured in retrolateral view and equals the distance from

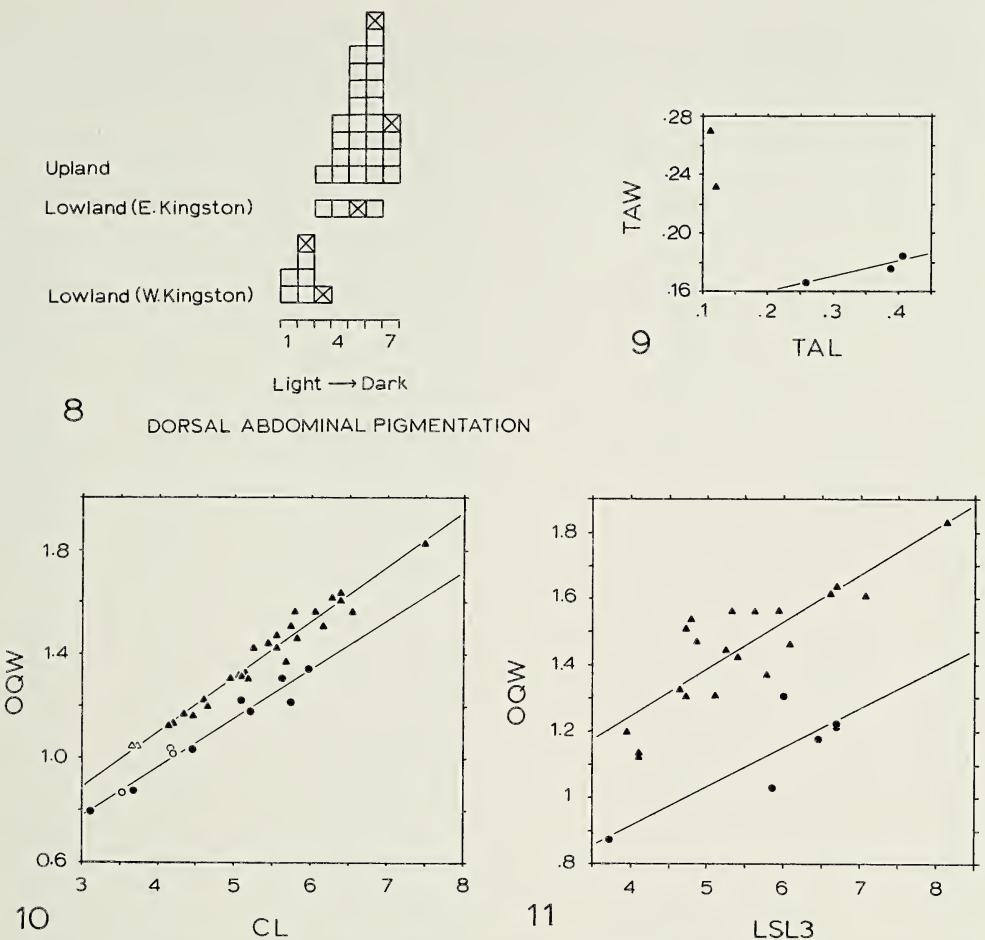


Figure 8.—Frequency distribution histogram of abdominal color variation in Jamaican *Ischnothele* species. Females designated by open squares, males by crossed squares. Figures 9-11.—Scattergrams for *I. reggae* (triangles) and *I. xera* (circles) with regression lines (values in mm); 9, males, TAW vs. TAL (*I. xera* regression: $y = 0.105x + 0.139$); 10, males (open symbols) and females (closed symbols), OQW vs. CL (*I. reggae* regression: $y = 0.212x + 0.253$; *I. xera* regression: $y = 0.188x + 0.214$); 11, females, OQW vs. LSL3 (*I. reggae* regression: $y = 0.142x + 0.678$; *I. xera* regression: $y = 0.118x + 0.446$)

the proximal point of articulation to the most distodorsal point of the article (in the case of IFL the distal point of measurement is the tip of the condyle, which is sometimes slightly proximal of the most distal point of the article). PL and PD were recorded after positioning the palpal organ for a retrolateral and slightly ventral view with the bulb and embolus tip in the same horizontal plane.

Measurements were performed with a Wild M-5® stereomicroscope with 20× eyepiece lenses and an eyepiece micrometer scale. LSL1, LSL2, and LSL3 measurements are accurate to 0.076 mm; SL (females), SW (females), ML, CFL, PFL, PTL, PTT, CYL, CYAL, PL, and PD are accurate to 0.018 mm; AMD, AMS, OQW, TAL, and TAW are accurate to 0.009 mm; all other measurements are accurate to 0.038 mm. All measurements are in millimeters.

Spermathecae were cleared in 85% lactic acid, viewed at 100-400× through a compound light microscope, and drawn with the aid of a drawing tube.

Table 1.—Quantitative character values for Jamaican *Ischnothele* males. Character abbreviations are defined in the Methods section of the text. All measurements given in millimeters. Range and mean given. ITSP, ITSR, TAS, CSP, and CSR values include data from both left and right appendages.

	<i>reggae</i> (N = 2)	<i>xera</i> (N = 3)	<i>reggae</i> holotype	<i>xera</i> holotype
MC	51,67	39-52(44.0)	67	39
ITSP	0-1(0.3)	2-4(3.0)	0,0	3,3
ITSR	0-2(1.3)	2(2.0)	1,0	2,2
TAS	7-9(8.5)	4-7(5.8)	9,7	4,4
CSP	0(0)	0-1(0.7)	0,0	1,1
CSR	0(0)	0-1(0.7)	0,0	1,1
CL	3.66,3.73	3.54-4.20(3.97)	3.73	4.16
CW	3.31,3.43	3.16-3.73(3.53)	3.43	3.70
AMD	0.19,0.20	0.17-0.19(0.182)	0.20	0.19
AMS	0.14,0.17	0.12-0.15(0.133)	0.14	0.12
OQW	1.06,1.06	0.87-1.04(0.974)	1.06	1.04
SL	2.04,2.08	1.89-2.31(2.17)	2.08	2.31
SW	1.58,1.73	1.54-1.96(1.81)	1.73	1.92
IFL	3.35,3.47	3.16-3.70(3.52)	3.35	3.70
ITL	2.73,2.73	2.46-2.93(2.75)	2.73	2.85
ITT	0.69,0.73	0.62-0.85(0.74)	0.73	0.85
IML	2.70,2.73	2.66-3.04(2.88)	2.73	2.93
MKP	1.08,1.08	0.92-1.16(1.07)	1.08	1.12
ITarL	2.54,2.54	2.16-2.89(2.61)	2.54	2.77
TAL	0.11,0.12	0.26-0.41(0.352)	0.12	0.41
TAW	0.23,0.27	0.17-0.19(0.176)	0.23	0.19
PFL	2.17,2.22	2.07-2.48(2.33)	2.17	2.48
PTL	1.63,1.65	1.48-1.74(1.64)	1.63	1.70
PTT	0.67,0.69	0.57-0.70(0.65)	0.67	0.70
CYL	1.48,1.55	1.44-1.85(1.67)	1.55	1.72
CYAL	0.81,0.94	0.83-1.11(1.01)	0.94	1.07
PL	0.83,0.85	0.76-0.89(0.84)	0.83	0.87
PD	0.48,0.48	0.46-0.52(0.49)	0.48	0.48
LSL3	3.47,3.47	3.70-3.85(3.77)	3.47	3.77
TAW(100)/TAL	193,243	45-64(51.7)	193	45
MKP(100)/IML	39,40	35-38(37.0)	39	38
OQW(100)/CL	28,29	24-25(24.6)	28	25
CS(100)/CW	14,15	18-22(20.6)	15	22

Each species description is a composite of all the adult specimens examined; these sample sizes are given in Tables 1 and 2. The quantitative character values recorded in these tables are an integral part of each description. Colors are described from specimens under alcohol, illuminated by a tungsten bulb, and viewed through a stereomicroscope.

For the analysis of variation of dorsal abdominal pigmentation, three of the preserved adult specimens in good condition were carefully selected to serve as standards: one with a relatively dark abdomen, one with a relatively light abdomen, and one with pigmentation intermediate between these two. These dorsal abdominal pigmentation values are the result of the distribution of two components: 1) pigments beneath the abdominal cuticle and 2) light and dark setae. The three standards were placed side by side in order of increasing

Table 2.—Quantitative character values for Jamaican *Ischnothele* females. Character abbreviations are defined in the Methods section of the text. All measurements given in millimeters. Range, mean, and standard deviation given.

	<i>reggae</i> (<i>N</i> = 23-27)	<i>xera</i> (<i>N</i> = 6-8)
CTP	6-12(8.8 ± 1.5)	8-10(9.3 ± 0.7)
CDP	0-3(0.6 ± 0.8)	0-4(0.9 ± 1.4)
CTR	9-12(10.0 ± 0.9)	7-9(8.4 ± 0.7)
CDR	8-18(13.1 ± 2.9)	10-16(13.8 ± 2.5)
PTarS	6-16(10.8 ± 2.2)	9-13(10.9 ± 1.6)
ITarS	2-7(4.3 ± 1.0)	5-11(6.3 ± 2.1)
MC	72-136(99.7 ± 18.7)	44-91(63.4 ± 18.6)
CL	4.14-7.49(5.45 ± 0.82)	3.12-5.97(4.86 ± 1.02)
CW	3.53-6.42(4.78 ± 0.69)	2.74-5.13(4.14 ± 0.85)
AMD	0.18-0.31(0.230 ± 0.032)	0.13-0.22(0.185 ± 0.031)
AMS	0.13-0.24(0.165 ± 0.029)	0.09-0.18(0.145 ± 0.034)
OQW	1.13-1.83(1.413 ± 0.179)	0.80-1.35(1.123 ± 0.200)
SL	2.15-3.80(2.87 ± 0.39)	1.72-3.05(2.58 ± 0.50)
SW	1.93-3.39(2.51 ± 0.32)	1.46-2.59(2.20 ± 0.40)
ML	1.24-2.26(1.65 ± 0.26)	0.89-1.66(1.38 ± 0.30)
CFL	0.47-1.24(0.78 ± 0.19)	0.35-0.91(0.61 ± 0.19)
IFL	3.23-5.74(4.17 ± 0.59)	2.32-4.26(3.55 ± 0.72)
ITL	2.28-4.03(2.93 ± 0.41)	1.60-3.08(2.52 ± 0.54)
IML	2.39-4.10(3.03 ± 0.42)	1.75-3.27(2.69 ± 0.57)
ITarL	1.48-2.36(1.87 ± 0.23)	1.10-2.01(1.65 ± 0.33)
LSL1	1.44-2.96(2.06 ± 0.32)	1.60-2.36(1.98 ± 0.25)
LSL2	1.29-2.89(1.84 ± 0.32)	1.37-2.28(1.90 ± 0.30)
LSL3	3.95-8.13(5.44 ± 1.08)	3.72-6.69(5.90 ± 1.12)
OQW(100)/CL	24-27(25.9 ± 0.9)	21-26(23.3 ± 1.3)
LSL3(100)/CL	81-111(97.3 ± 8.8)	101-132(118.6 ± 12.8)
OQW(100)/LSL3	23-32(27.1 ± 2.9)	18-24(19.6 ± 2.4)
AMD(100)/ITarS	3.5-9.6(5.7 ± 1.3)	1.9-3.8(3.1 ± 0.7)
ITarS(100)/CTR	17-67(43.4 ± 10.5)	56-157(76.6 ± 33.5)

darkness in an open petri dish of ethanol, which was illuminated by a 6 volt, 15 watt, Olympus TL stereomicroscope lamp positioned approximately 30 cm above the dish. All adult specimens were then individually placed in the dish, viewed close-up without magnification, and assigned an index of pigmentation, from 1 to 7, in the following manner: 1-abdomen lighter than the lightest standard; 2-abdomen like the lightest standard; 3-abdomen darker than the lightest standard and lighter than the intermediate standard; 4-abdomen like the intermediate standard; 5-abdomen darker than the intermediate standard and lighter than the darkest standard; 6-abdomen like the darkest standard; 7-abdomen darker than the darkest standard. This procedure was carried out independently by each author, using the same standards. For most specimens, both authors selected the same index. When the indices of a specimen differed by one unit, a coin toss decided the index. When the indices differed by two units (this happened for only two specimens), the mean was used as the index. Finally, if a specimen's abdomen was shrivelled and wrinkled, the index was lowered by one unit, and if an abdomen was covered by abnormal milky and glossy cuticle, its index was increased by one.

ANALYSIS OF VARIATION

The marked geographic variation in habitat and pigmentation observed by the first author while collecting Jamaican *Ischnothele* indicated that there might be more than one species of *Ischnothele* on the island.

The Blue Mountain populations (Fig. 7) are found at elevations of 3200-5000 feet in what Asprey and Robbins (1953) call upper montane sclerophyll forest and mist forest. The only other Jamaican *Ischnothele* specimen from an upland region is from Burnt Hill, located at an elevation of 1700-2000 feet in the Cockpit region where the principal natural community is wet limestone forest. Both the Blue Mountain and Burnt Hill populations experience over 80 inches of rainfall and only the briefest dry season each year. In contrast, the populations west and east of Kingston (Fig. 7) are situated on the dry south coast between sea level and 500 feet elevation in cactus thorn scrub and dry limestone forest, respectively. The former population receives less than 30 inches of rain per year and the latter less than 45 inches; both experience a long dry season of six to ten months. The mesic Blue Mountain forest habitat is characterized by a dense ground layer of vegetation and soils with considerable organic matter, whereas the coastal habitats have little or no ground vegetation and a rocky, porous, dry substrate, either solid, jagged, honeycombed limestone rock with almost no humus and scattered patches of leaf litter (west of Kingston), or loose limestone rock and gravel with only small amounts of organic matter and scattered patches of leaf litter (east of Kingston).

Because of the greater density of white setae and the lighter pigmentation under the abdominal cuticle, all adults from the lowland populations west of Kingston are much lighter (very light grey) over most of their body and appendages (Figs. 5, 6, 8) than the great majority of adults from the Blue Mountains and Burnt Hill, which are medium to dark brown (Figs. 3, 4, 8). The lowland sample from east of Kingston averages darker than the west of Kingston sample and lighter than the upland sample, and overlaps the pigmentation values of both those samples (Fig. 8).

The large habitat differences among these populations, especially between the upland and lowland populations, suggest that very different selection pressures may be acting on the different populations. The observations that 1) the coloration of each population approximates the substrate color characteristic of its habitat and 2) these spiders are often difficult to locate when they have been forced out of their webs by collectors and are on, or partly buried in, the substrate, are consistent with this hypothesis. Perhaps selection by visual predators is responsible for this color variation.

Unsuccessful searches for *Ischnothele* populations in two areas (see black bars in Fig. 7) of habitat intermediate in elevation, rainfall, vegetation cover, and substrate, and lying between the south coast and the backbone of the eastern mountain mass, suggest that the upland and lowland populations may be geographically isolated from each other by unsuitable habitat. These areas, along the Kingston to Newcastle road between Redlight and Mona and along the road from Port Morant to Bath and west of Bath, both provided geometrically suitable web sites (rock outcrops and earth road banks), but no *Ischnothele* webs were found.

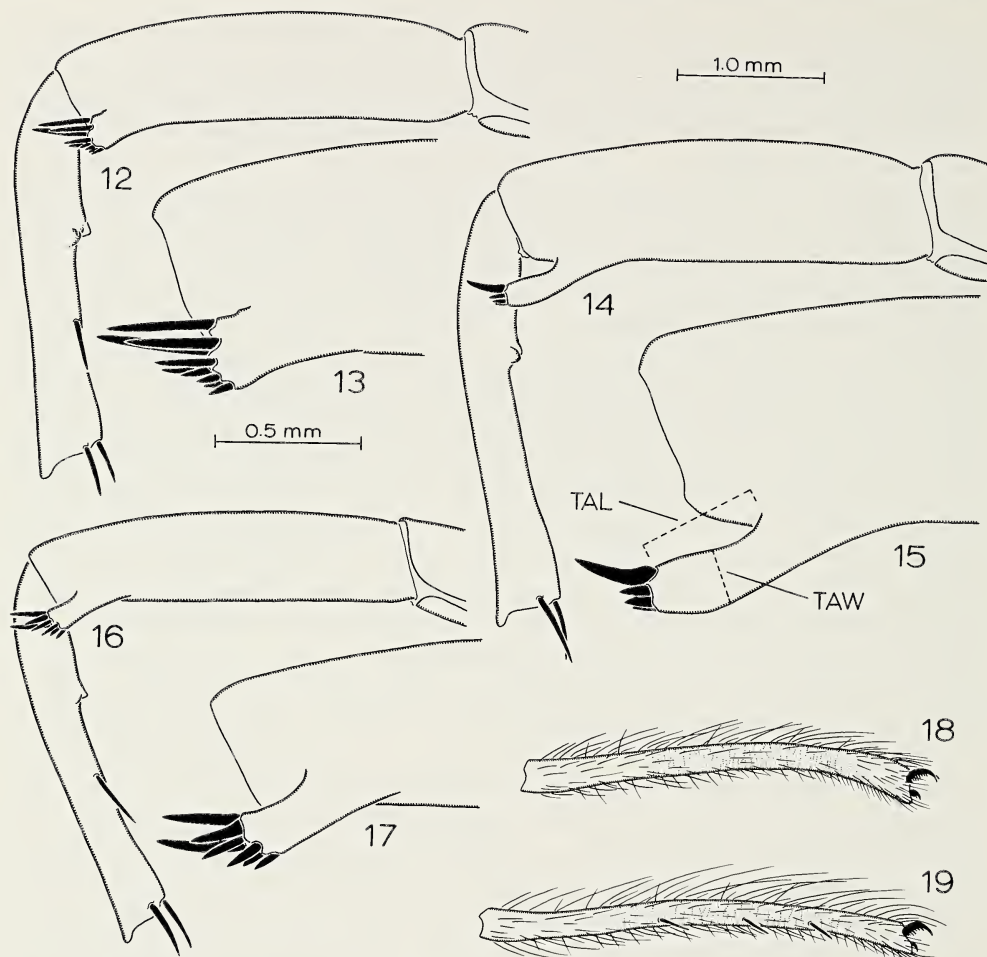
An additional finding also suggests to us that the Blue Mountain population and the lowland populations of *Ischnothele* are geographically isolated and have diverged genetically; each of these two population clusters harbors a different species of *Mysmenopsis* kleptoparasite which are each other's closest relatives (Coyle and Meigs 1989).

Our analysis of morphological variation in and among the *Ischnothele* samples also supports this hypothesis that the two lowland populations have diverged markedly from the upland populations, although it should be noted that especially small male sample sizes limit the rigor of this test. The results of this analysis are summarized below:

Males: Among the five available males, noteworthy (discontinuous) variation was observed only in some leg I, pedipalp, and eye characters. The tibia I apophysis of the three lowland specimens is considerably longer and more slender than that of the two upland specimens (Figs. 9, 12-17), but it is noteworthy that the east of Kingston male's apophysis (Fig. 16, 17) is not as long as those of the specimens from west of Kingston (Figs. 14, 15) and widens distally as in the upland males' apophyses (Figs. 12, 13) instead of being slightly constricted distally as in the west of Kingston specimens. Both west of Kingston males have a more prominent retrolateral metatarsal protuberance (Fig. 14) than do the east of Kingston (Fig. 16) and upland males (Fig. 12), and they also lack the ventroretrolateral spine that is present midway between this protuberance and the distal end of the metatarsus in the east of Kingston and upland males. The lowland males have more (2-4) prolateral spines on tarsus I (Fig. 19) than do the upland specimens (0-1) (Fig. 18). The lowland males (Fig. 23) have a deeper indentation on the ventral face of the palpal organ at the bulb-embolus junction than do the upland males (Fig. 22). For the east of Kingston male, the silhouette of the retrolateral surface of the embolus in ventral view is more similar to that of the other lowland males than to the upland males (Fig. 24), but the reverse is true of the silhouette of the prolateral surface. The two prolateral spines on the pedipalp patella are much thicker in the lowland (Fig. 26) than in the upland males (Fig. 25). In the lowland males, the more proximal of these spines is especially stout and tapers abruptly to an extremely thin deciduous tip. The ocular quadrangle of the upland males is proportionally wider than that of the lowland males (Fig. 10).

Females: For all meristic and measurement characters, there is considerable overlap among the samples of the three main population clusters (Blue Mountain plus Burnt Hill; west of Kingston; and east of Kingston). The least overlap is found in CTR (Table 2); all but two upland specimens have more retrolateral cheliceral teeth than all the lowland specimens. Several ratios separate some of the population clusters (Table 2): OQW(100)/LSL3 (Fig. 11), OQW(100)/CL (Fig. 10), AMD(100)/ITarS, ITarS(100)/CTR, and LSL3(100)/CL. For every one of these ratios the two lowland samples broadly overlap one another and are distinct from the upland specimens. The only quantitative character for which either lowland sample is even roughly intermediate between the other one and the upland sample is AMD(100)/ITarS, where most of the west of Kingston specimens are intermediate.

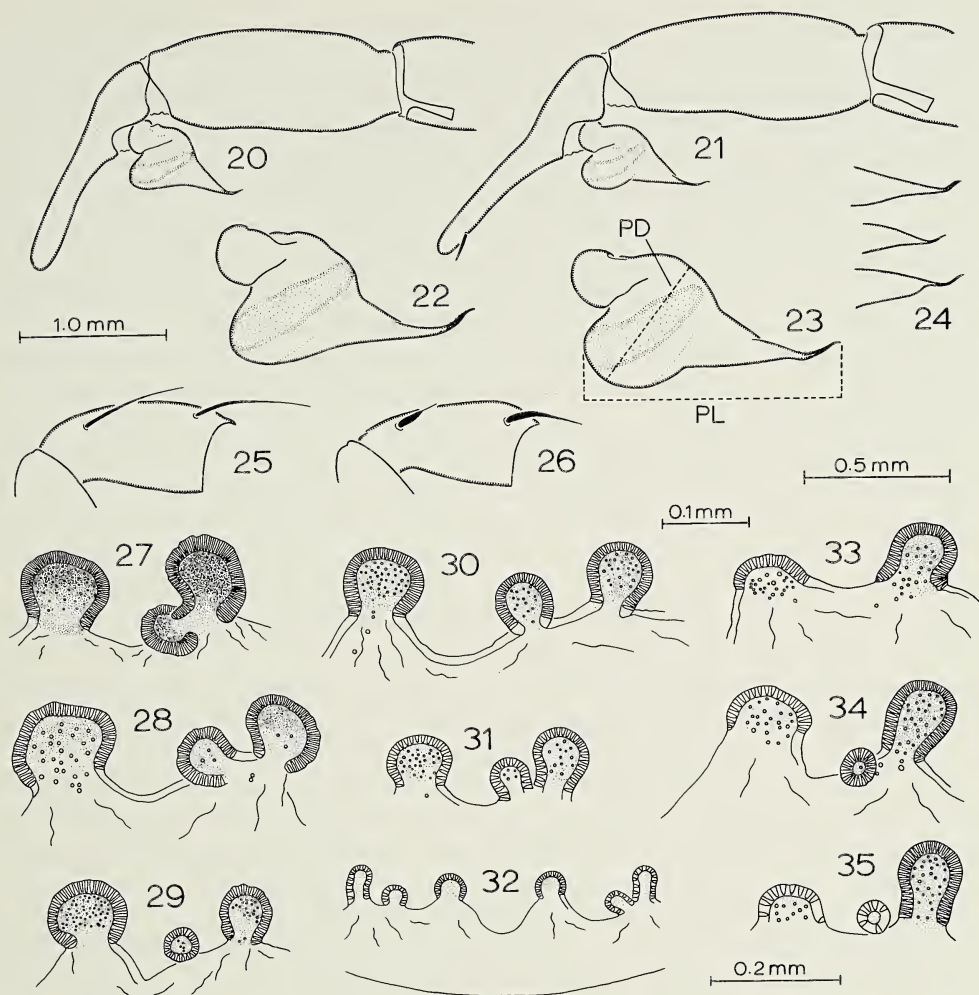
The females from west of Kingston all have distinctively low and relatively weakly sclerotized median bulbs which are much shorter than the lateral bulbs,



Figures 12-19.—Jamaican *Ischnothele* species, male leg I characters; 12, 13, *I. reggae* holotype, retrolateral; 12, tibia and metatarsus; 13, tibial apophysis; 14, 15, *I. xera* holotype, retrolateral; 14, tibia and metatarsus; 15, tibial apophysis; 16, 17, *I. xera* E. of Kingston, retrolateral; 16, tibia and metatarsus; 17, tibial apophysis; 18, 19, holotypes, tarsus, prolateral; 18, *I. reggae*; 19, *I. xera*. Scale lines: 1.0 mm for Figs. 12, 14, 16, 18, 19; 0.5 mm for Figs. 13, 15, 17.

and the secondary bulb between these two is small and not attached to the lateral bulb (or may even be missing) (Figs. 33-35). The upland females all have large, moderately heavily sclerotized median bulbs that are as tall or nearly as tall as the lateral bulbs, and the secondary bulb is usually, but not always, attached to the lateral bulb (Figs. 27-29). The spermathecal form of the specimens from east of Kingston (Figs. 30-32) is intermediate between those of these two samples, but appears closer to that of the upland sample than to the west of Kingston form.

In conclusion, the data available on variation in habitat, pigmentation, kleptoparasites, and morphology suggest that the Blue Mountain, east of Kingston, and west of Kingston populations have diverged genetically and that the latter two (lowland) have diverged less from each other than from the upland population. (The observation that the east of Kingston population is intermediate in several varying characters suggests that the three populations may be remnants of a once continuously distributed ancestral population that exhibited clinal



Figures 20-26.—Jamaican *Ischnothele* species male pedipalp characters; 20, 21, holotype tibia, cymbium, and palpal organ, retrolateral; 20, *I. reggae*; 21, *I. xera*; 22, 23, holotype palpal organ, ventral aspect of retrolateral; 22, *I. reggae*; 23, *I. xera*; 24, distal three-fourths of embolus, ventral view, *I. reggae* holotype (top), *I. xera* from E of Kingston (middle), *I. xera* paratype (bottom); 25, 26, patella, prolateral; 25, *I. reggae* holotype; 26, *I. xera*, E of Kingston. Figures 27-35.—Jamaican *Ischnothele* species female spermathecae; 27-31, 33-35, right side only, 32, both sides; 27-29, *I. reggae*; 27, Blue Mtns. 17 mi. post; 28, Whitfield Hall; 29, Catherine's Peak; 30-35, *I. xera*; 30-32, E of Kingston; 33-35, paratypes. Scale lines: 1.0 mm for Figs. 20, 21, 25, 26; 0.5 mm for Figs. 22-24; 0.1 mm for Figs. 27-31, 33-35; 0.2 mm for Fig. 32.

variation.) This indicates that it is more likely that intrinsic isolating mechanisms have evolved between the upland and lowland populations than between the lowland populations; consequently, we will describe two species of Jamaican *Ischnothele*, one from the uplands and one from the lowlands. We want to emphasize, however, that much more field work is necessary to gather enough data on geographic distribution, on variation in habitat, morphology, and other characters, and on reproductive behavior, to be able to rigorously test this and alternative hypotheses.

COEVOLUTION

Since the two Jamaican *Ischnothele* species are each other's closest relatives, since each harbors a different species of *Mysmenopsis* kleptoparasite, and since these two *Mysmenopsis* species are also each other's closest relatives (Coyle and Meigs 1989), it appears that these hosts and kleptoparasites have cospeciated. This is the first clear evidence for the kind of host-symbiont cospeciation process which Platnick and Shadab (1978) suggested might have played a role in *Mysmenopsis* evolution. Presumably, the ancestral kleptoparasite species was fragmented into geographically isolated populations on Jamaica as a result of fragmentation of the host *Ischnothele* population, and each set of host/kleptoparasite populations evolved independently in different environments under differing selection pressures.

The greater phenotypic difference (particularly in both male and female genital characters) between the two kleptoparasite sister species than between the two host sister species indicates that the former may have evolved more rapidly than the latter. Barnard (1984) lists four parameters which, if they differ between the host and parasite, may cause asymmetry in the rates of host and parasite evolution: population size, amount of variation within populations, the tendency of populations to become fragmented, and generation time. We lack enough information to evaluate the possible contributions of most of these and other factors to the apparently faster divergence of the *Mysmenopsis* populations, but we suggest that the probable difference in generation times between *Mysmenopsis* and *Ischnothele* could be one important factor. Like other tiny araneomorph spiders, these *Mysmenopsis* species probably have a generation time of no more than one year. Our observations of laboratory growth rates and size frequency distributions of *Ischnothele* species (including the Jamaican species) suggest that the Jamaican *Ischnothele* require 2 or 3 years to develop from egg to adult. Such a difference would mean a greater number of recombination and selection bouts per unit time in the *Mysmenopsis* populations than in the host *Ischnothele* populations; this would favor faster evolution of the kleptoparasite than the host.

Ischnothele reggae, new species

Figs. 1-4, 7-13, 18, 20, 22, 24, 25, 27-29

Types.—Male holotype and 12 female paratypes from roadbanks in humid montane forest along road between Newcastle (3800 ft. elev.) and Hardwar Gap (4000 ft. elev.), St. Andrew Parish, Jamaica (8 April 1988 [male molted to maturity on 24 April 1988]; F. Coyle, R. Bennett, and A. Robinson), deposited in the American Museum of Natural History.

Etymology.—The specific name is a noun in apposition taken from a popular genre of Jamaican folk music.

Diagnosis.—The two known males of *I. reggae* can be distinguished from the three known males of *I. xera* by the following differences: 1) The tibia I apophysis is shorter (Figs. 9, 12, 13) ($TAL = 0.11-0.12$) and wider ($TAW = 0.23-0.27$) [$TAW(100)/TAL = 193-243$] than in *I. xera* (Figs. 9, 14-17) [$TAL = 0.26-0.41$; $TAW = 0.17-0.19$; $TAW(100)/TAL = 45-64$]. 2) There are fewer prolateral spines on tarsus I (0-1) (Fig. 18) than in *I. xera* (2-4) (Fig. 19). 3) The two

prolateral spines on the pedipalp patella are much more slender and gradually tapering (Fig. 25) than in *I. xera* (Fig. 26), in which the more proximal of these spines is especially stout and tapers abruptly to an extremely thin deciduous tip. 4) The ocular quadrangle is proportionally wider [$OQW(100)/CL = 28-29$] (Fig. 10) than in *I. xera* [$OQW(100)/CL = 24-25$]. 5) The carapace edge setae are proportionally shorter [$CS(100)/CW = 14-15$] than in *I. xera* [$CS(100)/CW = 18-22$]. 6) Dorsal coloration is darker (Figs. 3, 8) than in *I. xera* (Figs. 5, 8).

Most females of *I. reggae* can be distinguished from those of *I. xera* by the following differences: 1) Since the ocular quadrangle is usually proportionally wider (Fig. 10) and the terminal article of the lateral spinneret is usually proportionally shorter than in *I. xera*, $OQW(100)/LSL3$ is the best ratio character for separating *I. reggae* (23-32) from *I. xera* (18-24) (Fig. 11). 2) CRT is usually greater (9-12) than in *I. xera* (7-9). 3) Because of their relatively high CTR and relatively low ITarS, *I. reggae* females usually have a lower value for $ITarS(100)/CTR$ (17-67) and a higher value for $AMD(100)/ITarS$ (3.5-9.6) than do *I. xera* females (56-157, 1.9-3.8, respectively). 4) Dorsal coloration is usually darker than in *I. xera* (Figs. 4, 6, 8).

Males.—Table 1. Palpus (Figs. 20, 22, 24) with large bulb rather clearly delimited from embolus base; ventral face of bulb-embolus junction only slightly indented; terminal one-third of embolus slender in lateral view, curved upward and retrolaterally, with abrupt downward bend just short of tip, with serrations along retrolateral aspect of dorsal surface. Pedipalp tibia (Fig. 20) subcylindrical with only slight ventral swelling in proximal half; no enciform spines. Spines on dorsal aspect of prolateral face of pedipalp patella slender, long, and gradually tapering (Fig. 25). Tibia I apophysis (Figs. 12, 13) short, broad, with numerous apical spines ranging from short to very long. Proximal one-third of metatarsus I (Fig. 12) with strong ventro-retrolateral depression delimited distally by prominent ventro-retrolateral protuberance associated with more prolateral ventral keel; distal end of metatarsus with ventral keel. Tarsus I flexible because of weakly sclerotized transverse "seams" over distal two-thirds (Fig. 18). Fovea a deep strongly procurved groove. One pair of long foveal setae. Bristles around lateral edges of carapace moderately long. Carapace pale yellow to orange yellow; chelicerae, pedipalps, and legs slightly darker. Abdominal dorsum with dark brown background color and 5-6 pairs of light areas; anterior pair largest, oval, joined by median pale area, other pairs (proceeding from anterior to posterior) progressively smaller, more obliquely transverse, more nearly united medially (Fig. 3). White setae not abundant.

Females.—Table 2. Spermathecae with two widely separated primary bulbs on each side and third, smaller, secondary bulb attached to (usually) or near lateral bulb (Figs. 27-29). Bulbs usually without stalks, heavily sclerotized; stalk, if present, short. Median bulb large, as tall or nearly as tall as lateral bulb. Fovea a deep strongly procurved groove (Fig. 1). One pair of long foveal setae (Figs. 1, 2). Bristles around edge of carapace moderately long (Fig. 1). Carapace pale yellow to orange-tan, similar to pedipalps and legs, lighter than chelicerae. Abdominal dorsum with medium to dark brown background color and 5-6 pairs of light areas as in males (Figs. 1, 4). White setae not abundant.

Variation.—See Analysis of Variation section above.

Natural history.—The *I. reggae* population observed between Newcastle and Hardwar Gap in the Blue Mountains favors road and trail banks in, or adjacent

to, moist forest. These banks range from low pebbly soil banks to high rock banks, some of which are exposed and considerably drier than others. Webs are abundant, reaching densities as high as five webs per m^2 on two different sections of tall roadbank. Collecting labels indicate that webs are sometimes constructed in bromeliads. The tubular silk retreats penetrate rock crevices, drill holes, soil cavities, moss, and leaf litter, and open out via one or two tubular access passageways onto exposed capture webs composed of one or two roughly horizontal sheets plus other non-horizontal sheets and strands (sometimes including vertical strands up to 30 cm long) anchored to surrounding substrates. A typical *I. reggae* web has a horizontal capture area of about 400 cm^2 , but this value ranges up to 1200 cm^2 in the largest webs.

The prey and prey capture behavior of *I. reggae* are described and discussed elsewhere by Coyle and Ketner (in press). In the field, these spiders appeared to be more reluctant to capture prey during the daytime than were other species of *Ischnothele* observed by the first author. *I. reggae* individuals run extremely fast (Coyle and Ketner in press) and/or feign death when forced out of their webs onto the ground; this plus their cryptic coloration makes them especially difficult to collect. *Mysmenopsis monticola* kleptoparasites were found in many of the larger *I. reggae* webs (Coyle and Meigs 1989).

Oviposition was observed in March, April, and May, but may not be limited to that period (A large number of third postembryonic instar spiderlings were collected with a female on 4 October 1957). As in the diplurid genus *Euagrus* (Coyle 1988), the bright white silk egg sac resembles a shallow silken bowl or short hammock holding the flattened spherical egg mass and covered with a layer of silk. It is usually suspended in the wall or floor of the tubular silk retreat. The *I. reggae* female tends to rest on the flat top of her egg sac (which is about as long as her body) or at least close to it, with her legs touching it. Of four egg sacs collected on 8 April, one contained only eggs, one contained only spiderlings in the second postembryonic instar (see Galiano 1972 for a description of postembryonic development in *Ischnothele siemensis*), one contained only fully active and pigmented spiderlings in the third postembryonic instar which appeared ready to abandon the egg sac, and one had recently been evacuated. Time from oviposition to evacuation of the egg sac ranged from 2.5 to 4 weeks in the seven broods produced in captivity. Brood sizes of the eight complete broods collected ranged from 47 to 100 and averaged 75.0. The three field-collected broods averaged larger (63-100; 85.6) than the five broods produced in captivity (47-100; 68.6). Within the first week after evacuating the egg sac, third postembryonic instar spiderlings did not capture prey (*Drosophila*) while in their mother's capture web even though they could move about quickly and spin silk. However, when such spiderlings were placed in individual containers, they constructed webs and captured and ate *Drosophila*.

Distribution.—Known from elevations above 1700 ft. in the Cockpit Country of western Jamaica and above 3200 ft. in the Blue Mountains of eastern Jamaica (Fig. 7).

Material examined.—The type specimens and the following: JAMAICA: PORTLAND PARISH; 17 mi. post, Blue Mountains, tree bases, 28 July 1955 (A. F. Archer and T. H. Farr), 1 female (IJ); Green Hills, 3750 ft. elev., 10 Sept. 1950 (Sibley), 1 female, juvs. (IJ); Hardwar Gap, 4000 ft. elev., 27 June 1954 (A. Chickering), 4 females, juvs. (MCZ). ST. ANDREW PARISH; Catherine's Peak, 5000 ft. elev., 26 June 1936, 1 female (USNM); between Catherine's Peak and Newcastle, road to Clifton Ht., 4000 ft. elev., 16 July 1950, juvs. (IJ); Cinchona, 4000 ft. elev., Jan. 1912 (C. T. Brues), 2 females

(IJ); Cinchona Plantation, road to Morce's Gap, 4000 ft. elev., 22 March 1940 (C. B. Lewis), 1 female (IJ); Clydesdale, 3500 ft. elev., 7 June 1948 (D. E. Miller), 1 female (AMNH); vicinity of Morce's Gap above Clydesdale, 4800 ft. elev., in bromeliads, 19 June 1948 (C. J. Goin), 1 female, juvs. (AMNH); just W of Silverhill Gap, 3250-3500 ft. elev., in bromeliads, 9 July 1952, 1 female, 1 male, juv. (AMNH); Yallahs River above Silverhill Factory, in bromeliads, 1 July 1952, juvs. (AMNH). ST. THOMAS PARISH; Farm Hill Gap, circa 4000 ft. elev., sheet web with funnel retreat in earth bank, 1 May 1950 (G. R. Proctor), 1 female (IJ); Whitfield Hall, 4200 ft. elev., under stones, 13 April 1950 (R. P. Benpury), 3 females, juv. (IJ). TRELAWNY PARISH; Burnt Hill, 1700-2000 ft. elev., under rocks, 21 July 1985 (G. B. Edwards), 1 female (FSC).

Ischnothele xera, new species

Figs. 5-11, 14-17, 19, 21, 23, 24, 26, 30-35

Types.—Male holotype and one male and four female paratypes from cactus thorn scrub at Fort Clarence (20-100 ft. elev.) and adjacent part of Hellshire Hills (20-200 ft. elev.) near Seafort, St. Catherine Parish, Jamaica (9 April 1988 [paratype male molted to maturity in Oct. or Nov. 1988]; F. Coyle, R. Bennett, B. Freeman, and A. Robinson), deposited in the American Museum of Natural History.

Etymology.—The specific name refers to the arid nature of this species' habitat.

Diagnosis.—Refer to the diagnosis for *I. reggae*.

Males.—Table 1. Palpus (Figs. 21, 23, 24) with large bulb sharply delimited from embolus base (ventral face of bulb-embolus junction strongly indented); terminal one-third of embolus slender in lateral view, curved upward and retrolaterally, with abrupt downward bend just short of slender tapered tip, with serrations along retrolateral aspect of dorsal surface. 0-1 enciform spines on prolateral and retrolateral surface of cymbium near tip. Pedipalp tibia (Fig. 21) subcylindrical with only slight ventral swelling in proximal half; no enciform spines. Spines on dorsal aspect of prolateral face of pedipalp patella basally thick; proximal spine especially thick, tapering suddenly to extremely thin deciduous tip (Fig. 26). Tibia I apophysis (Figs. 14-17) long, relatively slender, with few to many apical spines ranging from short to very long. Proximal one-third of metatarsus I (Figs. 14, 16) with strong ventro-retrolateral depression delimited distally by prominent ventro-retrolateral protuberance associated with more prolateral ventral keel; distal end of metatarsus with ventral keel. Tarsus I flexible because of transverse weakly sclerotized "seams" over distal two-thirds (Fig. 19). Fovea a deep strongly procurved groove. One pair of long foveal setae. Bristles around lateral edges of carapace very long. Carapace pale yellow to orange-yellow; recumbent white setae abundant (Fig. 5). Chelicerae, pedipalps, and legs similar to carapace. Abdominal dorsum with light to medium brown background color and 5-6 pairs of light areas; anterior 2 pairs largest, oval, joined by median pale area, other pairs from anterior to posterior progressively smaller, more obliquely transverse, more nearly united medially; numerous recumbent white setae (Fig. 5).

Females.—Table 2. Spermathecae (Figs. 30-35) with two widely separated primary bulbs on each side, usually with third smaller secondary bulb which may or may not be attached to lateral bulb. Bulbs usually without stalks; stalk, if present, short. Median bulb varies from low (much shorter than lateral) and weakly sclerotized to larger (nearly as tall as lateral) and moderately heavily sclerotized. Fovea a deep strongly procurved groove. One pair of long foveal

setae. Bristles around edge of carapace very long. Carapace pale-yellow to orange-tan; recumbent white setae usually abundant peripherally and sometimes elsewhere on carapace (Fig. 6). Pedipalps and legs similar to carapace, chelicerae darker. Abdominal dorsum (Fig. 6) with light grey-brown to medium brown background color and pattern of 5-6 pairs of light areas as in males; recumbent white setae numerous to abundant.

Variation.—See Analysis of Variation section above.

Natural history.—The populations studied west of Kingston live in hot, dry, cactus thorn scrub on honeycombed limestone substrate with very little soil. Webs are usually found where retreat tubes can penetrate the otherwise sparse leaf litter that accumulates at the bases of rocks and in some of the holes and crevices in the solid rock substrate. The population studied east of Kingston lives in dry limestone forest on a rocky hillside and is much denser than the population west of Kingston. The webs are most often at the bases of rocks, trees, and exposed roots and their retreats penetrate the loose limestone pebble substrate. *Ischnothele xera* webs are similar in shape to those of *I. reggae*, but tend to be smaller.

Prey capture behavior is described by Coyle and Ketner (in press). *Ischnothele xera*, like *I. reggae*, is reluctant to capture prey in daylight, is extremely fast, and sometimes feigns death when forced out of the web onto the ground. *Mysmenopsis furtiva* kleptoparasites were found living in the webs of adult *I. xera* (Coyle and Meigs 1989).

The adult male collected on 9 April west of Kingston was in the retreat of what appeared to be his own functional capture web. Four *I. xera* broods were collected on 9-10 April: one egg sac contained only spiderlings still in embryonic cuticle with split and wrinkled chorions still attached, one sac contained active third postembryonic instar spiderlings which were about to emerge from the sac, and two recently emerged and fully active third instar broods were found in their mothers' retreats. These stages conform to the pattern of early postembryonic development described by Galiano (1972) for *Ischnothele siemensis*. One *I. xera* female oviposited in captivity on 10 May. The two complete *I. xera* broods collected (both from the population east of Kingston) are larger (125 and 137) than all eight known *I. reggae* broods (47-100).

Distribution.—Known only from two areas of low elevation along the south coast of eastern Jamaica (Fig. 7).

Material examined.—The type specimens and the following: JAMAICA: ST. CATHERINE PARISH: Port Henderson Hill, 250-500 ft. elev., 21 August 1952 (G. Underwood), 1 female (MCZ). ST. THOMAS PARISH: route A4, 14-15 mi. E Kingston, about 300 ft. elev., dry limestone forest, 10 April 1988 (F. Coyle, R. Bennett, B. Freeman, and A. Robinson), 1 female, juvs. (AMNH); 14 mi. E Kingston, Morant Bay Road, below 250 ft. elev., 4 October 1957 (A. Chickering), 1 female, 1 male, juvs. (MCZ); 12 mi. E Kingston, about 200 ft. elev., 11 November 1957 (A. Chickering), 1 female (MCZ).

Note added in proof:

Three males, two from the *I. reggae* type locality and one from the *I. xera* type locality, have recently matured in our laboratory. With the following three exceptions, their character states lie within the ranges of the diagnostically useful characters of the previously studied conspecific samples: 1) The tibia 1 apophyses of the new *I. reggae* specimens are longer ($TAL = 0.14$ and 0.18 mm) and narrower ($TAW = 0.22$ and 0.20 mm), and thus the $TAW(100)/TAL$ values are considerably lower (160 and 116) than in the two conspecifics. 2) $OQW(100)/CL$

for the *I. xera* specimen is 26, which is slightly higher than that of its three conspecifics. 3) Two of the new males have similar CS(100)/CW values (*I. reggae* = 16.7, *I. xera* = 17.3) which lie between the ranges of the two previously described species samples. These new data reduce the usefulness of two of the seven diagnostic characters that separate the males of *I. reggae* and *I. xera*, however they are consistent with the hypothesis that these are different species.

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RESEARCH NOTES

**AN EXAMPLE OF PARTIAL DUPLICATION OF
THE ABDOMEN IN *NEOBISIUM SIMONI*
(PSEUDOSCORPIONES, NEOBISIIDAE)**

Records of abdominal anomalies in the pseudoscorpion family Neobisiidae are very sparse in the older literature (Kästner 1927; Pedder 1965). Only recently, comparative aspects of teratological variation have been studied in six European species belonging to the genera *Neobisium* Chamberlin and *Roncus* L. Koch (Čurčić 1980, 1989; Čurčić and Dimitrijević 1982, 1984, 1985, 1986; Čurčić et al. 1981, 1983). These studies have revealed the outstanding heterogeneity of segmental anomalies affecting abdominal sclerites in the species analyzed. The sclerite deficiencies in different species of the family Neobisiidae have been found mostly in the adult stage or occasionally in the tritonymph (Čurčić 1989). No deficiencies have been observed in the preceding instars (deutonymph and protonymph).

In a collection of pseudoscorpions made by one of us (RND) at Passarole, near Moulis (Ariège), France, during July 1987, one anomalous protonymph of *Neobisium simoni* (L. Koch) was collected. This specimen was obtained from the leaf litter and humus in a mixed oak forest. In the protonymph studied, only the dorsal sclerites were aberrant, the ventral sclerites and the appendages were normal in all respects.

The aim of this note is to describe the phenomenon of tergal teratology of the aberrant protonymph. All tergites of this specimen are anomalous (Fig. 1). Thus, tergite I lacks a section on the right; in addition, the number of setae on this sclerite is reduced. Abdominal tergites II-VI are duplicated on either side of the mid-line (thus forming separate "demi-tergites"), and their form and distribution are drastically changed in relation to those in normal protonymphs of *N. simoni*. Tergite VII is fused with the left part of tergite VIII and as well as with the right section of tergite IX. An isolated section of tergite VIII is present on the right. Furthermore, tergites VIII-IX and IX-X have developed a bicyclical sinistral helicotomy. An isolated part of tergite X is present on the left. As a consequence of the deficiencies noted, the tergal setation in this specimen is significantly altered in relation to normal setal complement (which is, for tergites I-X, 4-4-4-4-4-4-4-4-4-4). Altogether, five types of teratologies have been found to affect the abdominal tergites in this protonymph: hemimery, atrophy, symphysomery, helicotomy and tergite enlargement.

The majority of the abdominal deficiencies in neobisiid species occur during the transformative development of tritonymph into adult (Čurčić and Dimitrijević 1986). It appears likely that the origin of such anomalies may be induced by some irregularity in the process of molting. Considerably fewer specimens become

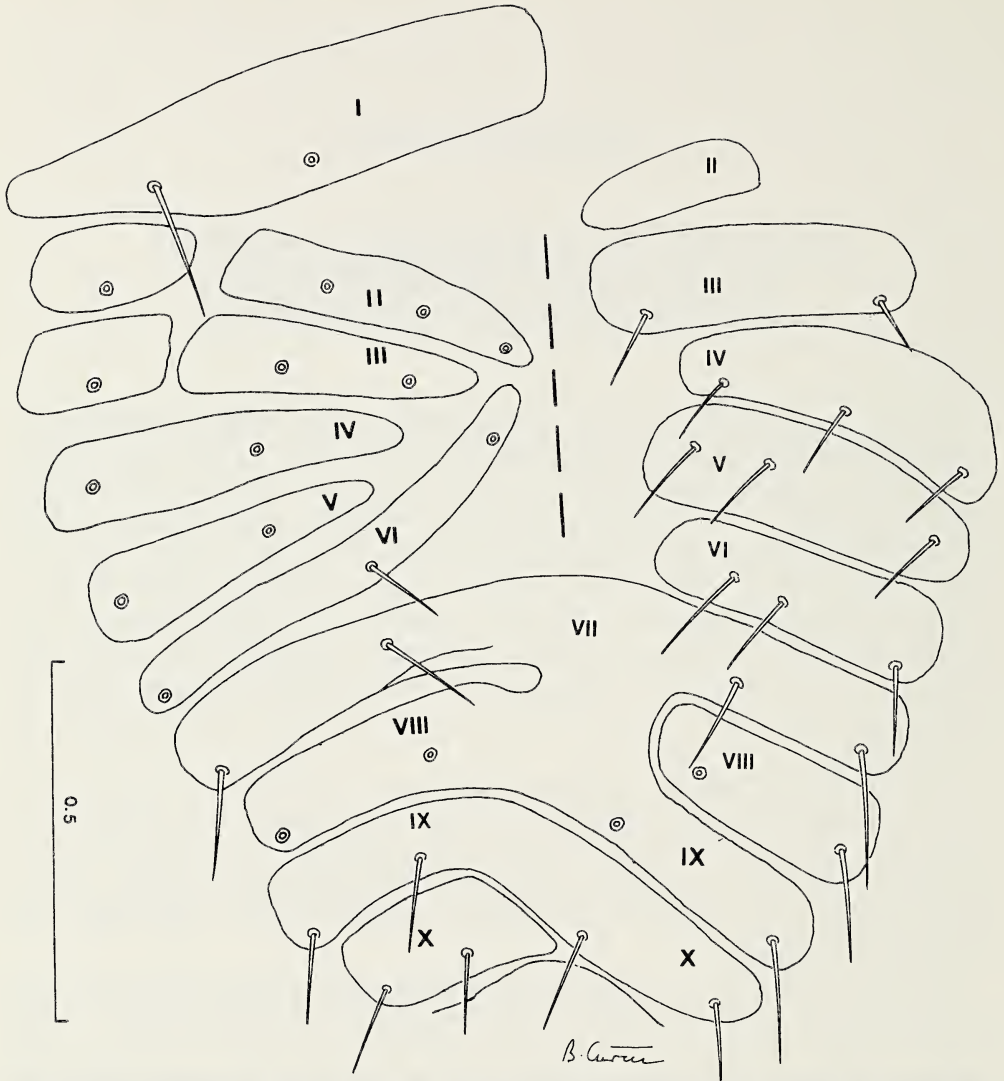


Figure 1.—*Neobisium simoni* (L. Koch). Tergites I-X, protonymph from Passarole. Scale bar in mm.

anomalous when transforming from deutonymph into protonymph (Ćurčić et al. 1983), or even from the protonymph into deutonymph stage, as was shown by Pedder (1965) for representatives of families other than Neobisiidae.

Since the aberrant example of *N. simoni* is a protonymph, the genesis of its deficiencies remains obscure. However, one may assume that the origin of the drastically modified abdominal tergites in this specimen could be found among the genetical (or some morphogenetic) factors, which influence the pre-molting period of the ontogenetic process.

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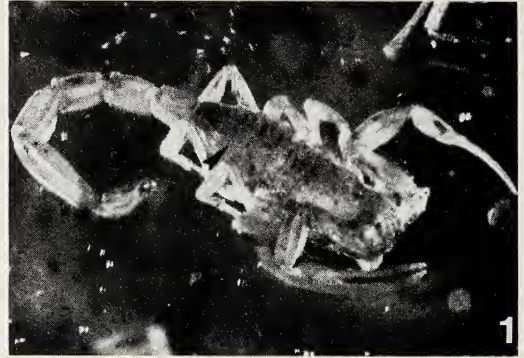
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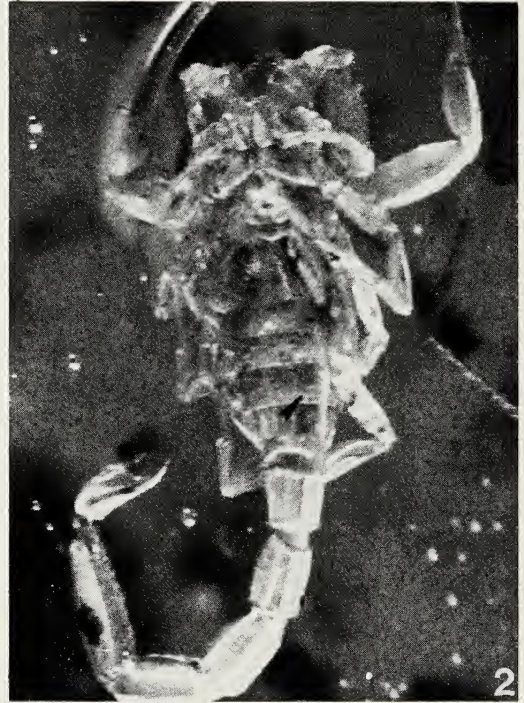
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A NEW SPECIMEN OF *MICROTITYUS AMBARENSIS* (SCORPIONES, BUTHIDAE), FOSSIL FROM HISPANIOLA: EVIDENCE OF TAXONOMIC STATUS AND POSSIBLE BIOGEOGRAPHIC IMPLICATIONS

Three fossil buthid scorpions have been described from Hispaniola, all from single juveniles embedded in Dominican amber: *Centruroides beynai* Schawaller, 1979, *Tituyus geratus* Santiago-Blay and Poinar, 1988, and *T. ambarensis* Schawaller, 1982. Whereas in the type species of the genus, *Microtityus rickyi* Kjellesvig-Waering, 1966, femoral trichobothrium d₂ is absent, *M. ambarensis* bears it, providing one of the main reasons for its original placement in *Tityus*. Scrutiny by several researchers led to the suspicion that *T. ambarensis* may belong to *Microtityus* Kjellesvig-Waering, 1966. Armas (1988) transferred *T. ambarensis* to *Microtityus* without having available the holotype or other specimens (Armas to Schawaller 29 May 1987; Schawaller to Armas 8 July 1987; in litt.). Evidence from a new fossil specimen now supports the placement of *T.*



Figures 1, 2.—*Microtityus ambarensis* (new specimen): 1, dorsal view, note three dorsal mesosomal keels (arrowhead points one keel); 2, ventral view, note suboval spiracles (arrowhead points one spiracle).



ambarensis in *Microtityus*. We also discuss possible biogeographic interpretations of this find in light of a vicariance model.

The new scorpion, which is 7.6 mm long, is in a piece of amber believed to have come from La Toca mine, Northern Dominican Republic. Amber from that mine has been dated as approximately 30-40 million years old (Lambert et al. 1985). The exact origin of the amber piece with the holotype of *T. ambarensis* is not clear. Based on the ratio of the overall total lengths (1.2), we conclude that the new specimen is a second instar, one instar less than the holotype. Two of the three dorsal mesosomal keels are evident (Fig. 1) and the spiracles are relatively small and suboval (Fig. 2); these are critical qualitative generic characters obscured in the holotype (Armas 1988). The dentition of the pedipalp movable finger is almost non-overlapping and there is a small pectinal tooth count (10-11, for this species), as typical of *Microtityus*. The full complement of pedipalp femoral trichobothria present in this specimen distinguishes the taxon from the small South American buthid *Mesotityus* González-Sponga, 1982. The holotype

was, in contrast to its description, originally illustrated with eight, instead of seven, mesosomal tergites (Schawaller 1982).

With the exception of *M. ambarensis*, all other described species of *Microtityus* are extant; all are small (< 25 mm long at adulthood). *Microtityus ambarensis* can be distinguished from *M. dominicanensis* Santiago-Blay, 1985 and *M. consuelo* Armas and Marcano Fondeur, 1987 by the number of pedipalp finger rows and pectine tooth number: *M. dominicanensis* has 10 rows and 8 teeth; *M. consuelo* has 11 rows and 14 teeth.

The genus *Microtityus* is neotropical buthid taxon known from Brazil, Venezuela, Trinidad, Virgin Islands, Dominican Republic, Haiti (Santiago-Blay, in prep.), and Cuba. The genus has not been reported for Jamaica, Puerto Rico or the Lesser Antilles. We suggest that when the Caribbean plate(s) first contacted the South American plate about 60-80 mya (Pindell and Barrett, in press), ancestors of today's Caribbean *Microtityus* fauna migrated from the south. However, although the Caribbean plate seems to have been in contact with continental land masses, direct dry land connections have not been proven. We cannot indicate whether the arrival of *Microtityus* to the area was a product of vicariant or dispersal events. Further splitting and accretion of the Greater Antilles land masses produced subsequent vicariant events responsible for the development of a 100% endemic *Microtityus* fauna.

J. Yellen kindly allowed author JASB to study the specimen and provided the data on the probable collection site of the new fossil piece. P. Craig and J. Yellen did the photographic work. E. E. Williams, M. Perfit, J. L. Pindell, G. A. Polis, W. D. Sissom and S. Stockwell reviewed the manuscript and suggested changes. The authors are most grateful to them all.

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A ZYGOMYCETOUS FUNGUS AS A MORTALITY FACTOR IN A LABORATORY STOCK OF SPIDERS

The first instars of our laboratory stocks of several spider species are usually fed with fruit flies, *Drosophila melanogaster*. In 1987 and 1988, we noticed a disease in several hatchling groups of *Cupiennius salei* Keyserling (Ctenidae) and *Ischnothele guyanensis* Walckenaer (Dipluridae). The spiders did not accept food and did not move very much. They sat most of the time on the bottom of the box (instead of hanging under the lid) and their appearance became dark and wet. Such spiders died 2-6 weeks after these symptoms were recognized.

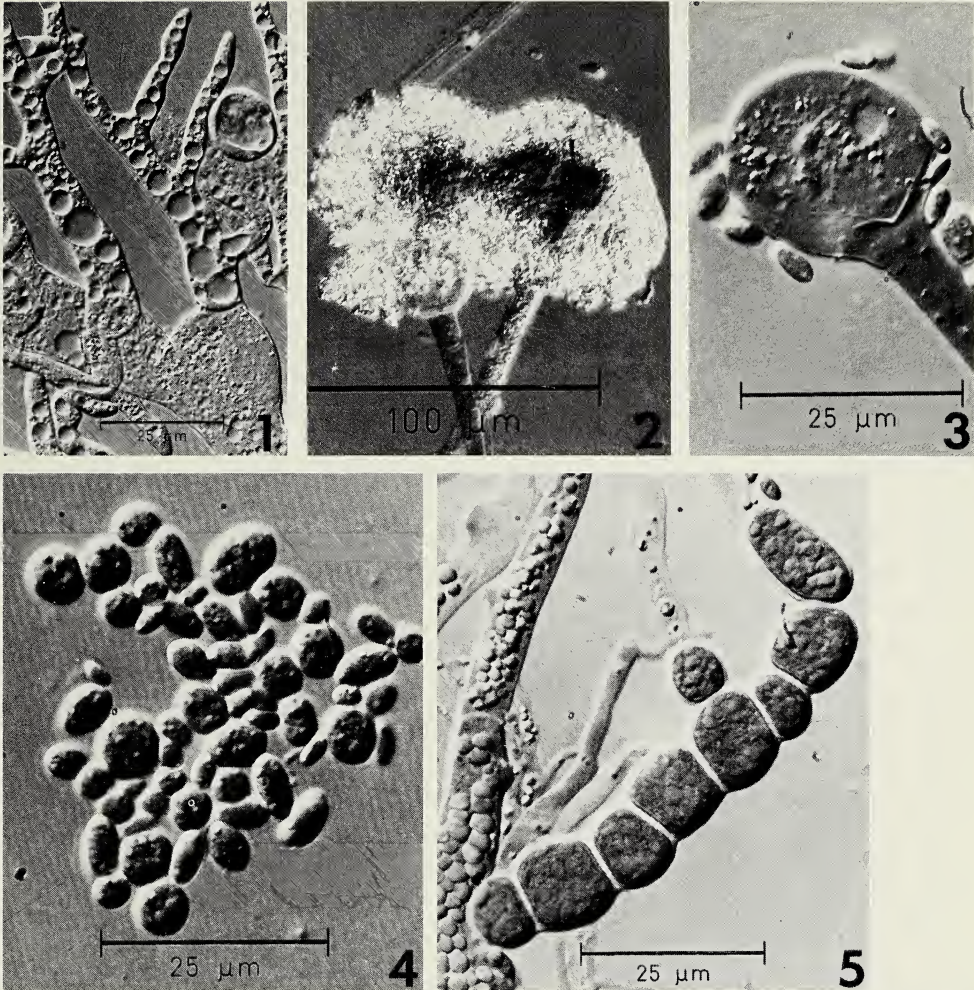
The infection rate of a given hatchling group (50-100 spiderlings) was about 90-100% and probably all infected spiders died (total *N* of dead spiders >500). We do not know whether the surviving spiders had not been infected or whether they successfully fought the infections. When the disease was recognized at an early stage, some techniques could increase the survival rate to approximately 20-30%. We tried several breeding techniques and found the following methods to lower spider mortality: Low air humidity (<70%), no free water, cleaning the box once a week, lids with additional slits to provide a better air circulation and no *Drosophila* food. The relative success of our changed breeding technique indicated that our spiders had probably been infected by a pathogen which originated from our *Drosophila* culture. Since *Drosophila* vials house a wide range of fungi in the food medium of the larvae, it is possible that the flies function as a vector for these pathogenic fungi when fed to the spiders.

To test this assumption we anaesthetized a total of 22 *Ischnothele* and 8 *Cupiennius* from different breeding groups by CO₂, cut off the opisthosoma under sterile conditions, disinfected the cuticle with ethanol (70%), opened the body ventrally with fine scissors and took a tissue sample with a sterile needle. The tissue was inoculated on Petri dishes and cultured on malt agar at 20° C. After 1-2 days the first fungal colonies could be detected. For further identification some fungus colonies were selectively transferred to new Petri dishes and cultured and propagated as above.

From all spider samples we were able to isolate the zygomycete *Mucor hiemalis* f. *hiemalis* (Figs. 1-5). This identification was confirmed by W. Gams and M. A. A. Schipper. This fungus is distributed worldwide and common in the soil or on plants (Zycha et al. 1969). It is known to kill honey bees (Burnside 1935) and several Lepidoptera, Coleoptera and Diptera species (Heitor 1962), but causes also a tomato disease (Zycha et al. 1969).

From some spider samples we could further isolate an unidentified fungus imperfectus. In nearly all spiders high numbers of bacteria were found. A microscopic examination of the tissue sample soon after the dissection of the spider revealed that the intestinal tract of most spiders contained up to three different bacterial forms. We did not make further efforts to identify them.

How does the fungus infect the spider? Since the spiders feed on infected *Drosophila* flies, we first thought that the fungus enters the spider's body via spores which survive the extraoral ingestion and pass through the prosoma filter system. An inhibition test with a suspension of *M. hiemalis* spores (10⁶ spores/ml) on agar plates and 2µl digestive fluid of *Cupiennius* did not prevent the



Figures 1-5.—The zygomycete *Mucor hiemalis* f. *hiemalis* Wehmer, isolated from a laboratory stock of spiders (interferential contrast microscope): 1, the primitive siphonal mycelium, grown from sporangiospores in a submers culture; 2, two sporangia with a dissolved sporangial wall; 3, empty sporangium, columella with remnants of the sporangium wall; 4, sporangiospores of different sizes; 5, spherical gemmae at older mycelium (slide culture).

spores from germinating. This indicates that *M. hiemalis* spores could survive the ingestion by a spider, although the digestion of fungus spores could be shown for orb-weaving spiders (Smith and Mommsen 1984). But could the spores pass through the prosoma filter? Though particles $>1\ \mu\text{m}$ are normally retained by the effective filter system, larger particles such as pollen or spores can pass it as well (Collatz 1987). To test this assumption, we injected $20\ \mu\text{l}$ of a spore suspension (10^6 spores/ml) into crickets which were fed to spiders. We chose spores of varying size (from 1 to $10\ \mu\text{m}$) from three fungus species: two tropical fungi (to exclude possible error and interpretation problems) and *M. hiemalis*. The spiders ($N = 15$) were killed and tissue samples from the opisthosoma and prosoma (behind the filter) were inoculated on malt agar. In no case could fungal growth be observed. This indicates that the infection by *M. hiemalis* spores probably does not occur during the normal feeding procedure.

Greenstone et al. (1987) succeeded in infecting spiders with the pathogenic hyphomycete *Nomuraea atypicola* by topical application of a spore suspension and Heitor (1962) mentions that *M. hiemalis* can infect insects through injuries. So it is possible that the infection by this fungus occurs through microscopic lesions of the cuticle or other sensitive openings (book lungs?).

Is the infection of spiders by *M. hiemalis* a mere laboratory effect caused by contact with infected food items or does it occur regularly among free-living spiders as well? To answer this question we collected 10 spiders representing 10 different species from other parts of the building where our laboratory spiders were bred (*Pholcus phalangoides* (Fuesslin) (Pholcidae), *Dysdera crocata* C. L. K. (Dysderidae) and *Tegenaria* sp. (Agelenidae)) and from nearby parts of the campus (*Argiope bruennichi* (Scopoli), *Larinioides cornutus* (Clerck) *Araneus diadematus* Clerck (Araneidae), *Pisaura mirabilis* (Clerck) (Pisauridae), *Linyphia triangularis* (Clerck) (Linyphiidae), *Clubiona* sp. (Clubionidae) and *Xysticus* sp. (Thomisidae)). The spiders were treated as mentioned above and malt agar Petri dishes were inoculated. In no case could any fungal growth be found. This probably indicates that the infection by *M. hiemalis* is restricted to our laboratory stock, although the wide dispersion of the fungus could enable it to be a more common pathogen of spiders.

At the end of 1988, the complete laboratory stock of *Cupiennius salei* was moved from Regensburg to Bern. The spiders were housed in rooms where no *Drosophila* have been bred before. All plastic containers were replaced by new materials and the spiders were exclusively fed with crickets. Under these conditions no fungal disease of the previous epidemic dimension could be observed and the survival rate of hatchlings was about 90-100% during the first 3-4 instars ($N > 800$). This can be understood as a further argument for a correlation between *Drosophila* food, fungal infection and spider mortality (though it does not prove a cause and effect relationship).

Until now true pathogenic fungi of spiders were only known from Ascomycetes (the genera *Cordyceps* and *Torrubiella*, Clavicipitales) and from their hyphomycete anamorphs (*Gibellula*, *Nomuraea* and 7 other genera), the imperfect fungi (Nentwig 1985; Evans & Samson 1987). No fungi pathogenic to spiders are known from the Myxomycetes or from the Basidiomycetes. The herein reported case of *M. hiemalis* is probably the first observed pathogenic example from the Zygomycetes. Although we present here only a laboratory case, it is possible that Zygomycetes infect spiders under natural conditions as well. An interesting feature of the zygomycete pathogens is the apparent lack of host specificity. According to our knowledge, pathogenic fungi of spiders do not infect insects and the insect pathogenic fungi (e.g., Entomophthorales) do not infect spiders (Evans and Samson 1987). In contrast to this, *M. hiemalis* seems to have a wide host range and includes insects and spiders.

We thank W. Gams and M. A. A. Schipper for the confirmation of the fungus identification and critique of an earlier draft, B. Kellerer and Th. Forst for technical assistance.

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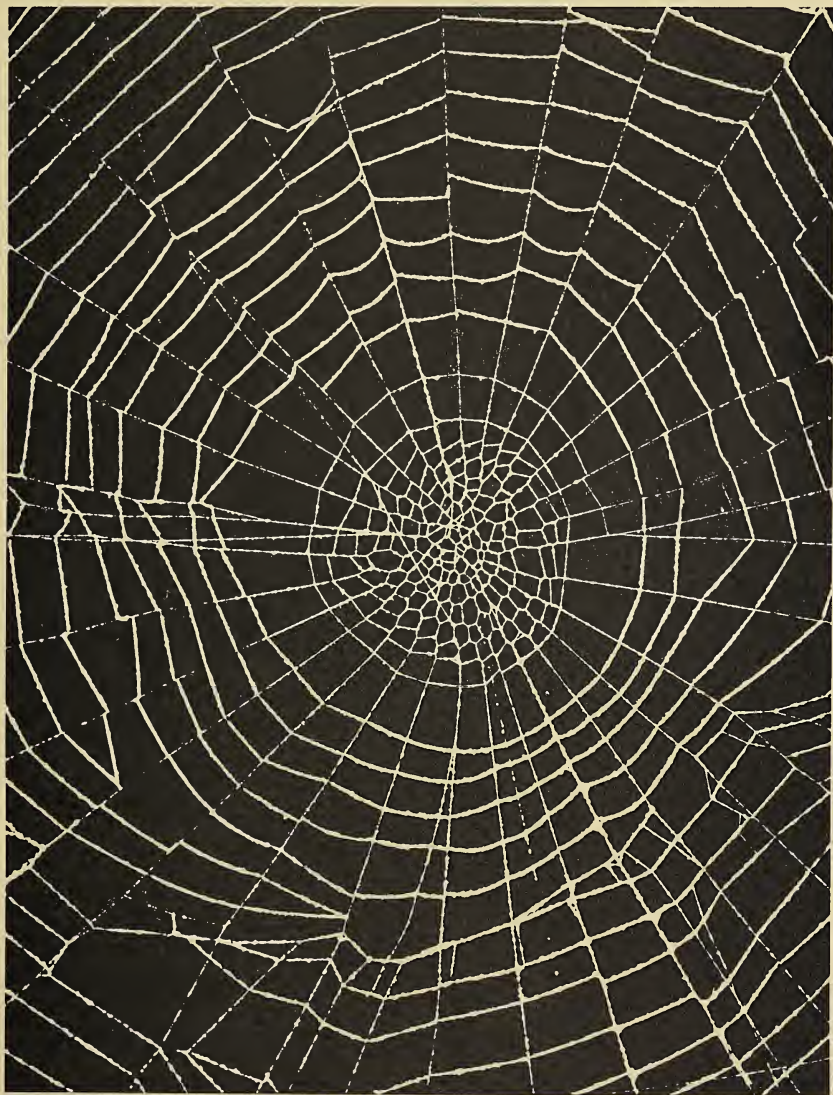
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ANNUAL ACTIVITY PATTERNS OF THE AUSTRALIAN TARANTULA *SELENOCOSMIA STIRLINGI* (ARANEAE, THERAPHOSIDAE) IN AN ARID AREA

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ABSTRACT

Activity patterns of a population of the burrow-dwelling theraphosid spider, *Selenocosmia stirlingi* Hogg, at Coombah (N.S.W.) are reported. Burrows were located and monitored at about 6-weekly intervals over a period of 3 years while rainfall and diurnal temperature profiles of the soil were also recorded. Spider activity was determined both from the condition of the burrow entrance and from the presence of the spider at the burrow entrance during the night. Activity was greatest in spring and late summer/fall, with low levels of activity in both winter and mid-summer. It is likely that the temperature profile in the soil was exploited behaviorally by the spiders in order to thermoregulate. Estimated losses of spiders from the population were greatest in spring and early summer, and may be due predominantly to maturing males leaving their burrows in search of females.

INTRODUCTION

Stradling (1978) determined that the tarantula *Avicularia avicularia* Linnaeus matured in 3-4 years in the tropical conditions of Trinidad, compared to a projected development period of 10 years for an arid zone species, *Dugesiella hentzi* (Girard), in Arizona (Baerg 1958). Stradling's (1978) data showed that the variation in size increase and instar duration increased as the spiders grew. It therefore seemed likely that environmental factors, such as food availability (e.g., Turnbull 1962, 1965), temperature (e.g., Peck & Whitcomb 1970) and photoperiod (Peck & Whitcomb 1970) might cause these accumulated differences.

In Australia, *Selenocosmia stirlingi* Hogg occurs throughout arid areas in the center of the continent, and its range extends into northern tropical regions (Main 1964). The environmental variation across its range suggested that it would be an appropriate candidate for the investigation of phenotypic plasticity in growth and development. Investigations of the field ecology of *S. stirlingi* formed part of a broader study of the influence of environmental factors on the spider's growth and development (Kotzman 1986). The field study described here was undertaken to characterize the arid environment in which these spiders live (particularly in terms of temperature) and to establish the spiders' natural activity patterns in the context of these conditions. As these spiders occupy deep burrows and forage nocturnally from the burrow entrance, "activity" was measured by

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indications of the spider's use of the burrow entrance. Diurnal variations in soil temperatures were recorded, rainfall records were obtained from the nearby homestead, and the condition of marked burrows and activities of their occupants were monitored. From these observations, a general picture of the relationships between the activities of the spiders and the changing environmental conditions was derived.

STUDY AREA AND METHODS

Distribution of *S. stirlingi* is patchy, and only after thorough searching was a study site chosen (about 180×450 m) about 5 km south of the Coombah homestead, on the east side of the Silver City Highway 136 km north of Wentworth (New South Wales). The site consisted of a central swale bordered on the north and south by sandhills, and to the east by a claypan, with a total relief of about 7 m (Fig. 1). Ground cover varied enormously during the study, from virtually none to dense grasses and herbs. In general, vegetation of the area is described as a Belah-rosewood community, including scattered trees (*Casuarina* sp.) about 100 m apart, with "blue bush", herbs and grasses beneath (Cunningham et al. 1981). During each visit, at approximately 6-week intervals, new burrows were located by systematically searching the length and breadth of the field site. Each new burrow was marked with a wooden stake (placed 150 mm west of the burrow) and numbered sequentially as it was found. The condition of all burrow entrances was assessed and the presence or absence of the spider (and juveniles) at the entrance at night was noted. Burrow diameter was measured to the nearest mm using a dial caliper (Mitutoyo Co.) and depth was determined to the nearest cm by inserting a length of rubber into the burrow. In a nearby area, fifteen burrows were excavated to determine their structure and to collect spiders for laboratory experiments.

A planimetric map of burrows and other major features in the site was produced with a telescopic level (Fuji Corp.) and a pair of plane tables. Spot heights were measured along a series of levelled transects and the contours interpolated between them were converted to altitudes above sea level using a Special Survey mark (SSM 3910, $33^{\circ}01'$ South, $141^{\circ}38'$ East) located within the site. The distribution of burrows within the site was compared with the values expected with a low frequency, discrete, random distribution (Poisson) and a coefficient of dispersion (*C.D.*) was calculated (Sokal & Rohlf 1969).

Rainfall data were obtained from a plastic wedge rain-gauge at the Coombah Homestead (5 km north of the field site). Solid state temperature sensors (AD590JH) connected to a 4-channel Rustrak™ recorder (Galton Inc., U.S.A.) were used to monitor field temperatures for 24 h during each visit. Initially two sensors were buried at 25 and 60 cm and allowed to equilibrate for 6 weeks. The temperatures recorded with buried sensors were the same as those from sensors at similar depths within burrows. Therefore, sensors were buried at the surface, 20 cm and 60 cm for the remainder of the study to determine burrow temperatures.

Spider activity was assessed in terms of the burrow entrance condition ("open" or "closed") and the presence or absence of the spider (and any juveniles) in the top of the burrow at night ("seen" or "not seen"). Evidence of the seasonality of male mate-seeking activity was obtained from the records accompanying the 16 male specimens of *S. stirlingi* held in the South Australian Museum, one

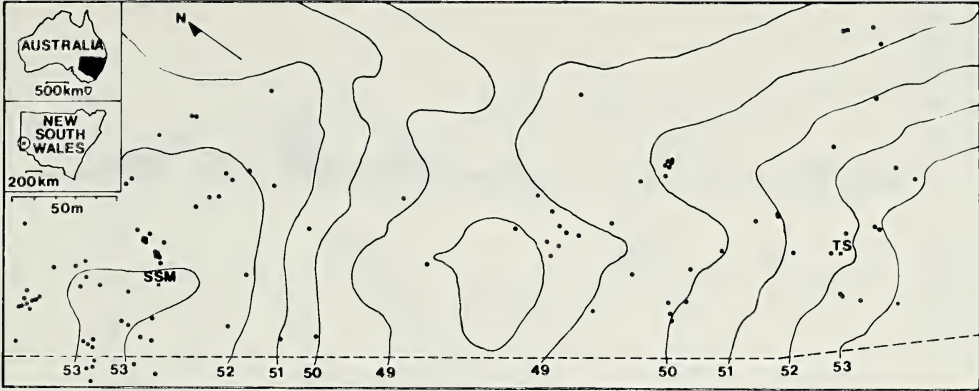


Figure 1.—Location and map of the field study site at Coombah (N.S.W.): spider burrows (dots), 1 m contours (solid lines, heights above sea level), roadside fenceline (broken line), buried temperature sensors (TS) and Special Survey Mark (SSM).

specimen collected at the Coombah Homestead during the study, and the type specimen from the British Museum (Natural History).

RESULTS

Conditions in the field area.—Daily rainfall records were combined to produce monthly totals (Fig. 2). Average annual rainfall during the study ranged from 130.0–408.3 mm, with no rain falling in 10 of the 37 months. The rainfall pattern observed during the study was typical of this region and compared well with longer-term figures from Menindee (100 km northeast of Coombah) where annual falls have ranged from 52–766 mm and the mean is 236 mm (Cunningham et al. 1981). At Coombah the mean annual rainfall over the 3 years was 232 mm, and thus biotic activity related to rainfall (including spider activity) can be considered typical of the area.

The diurnal temperature ranges were greatest at the soil surface (up to 45°C), less at 20 cm (typically 5–7°C) and least at 60 cm (no more than 2°C) (Fig. 2). The trends for annual ranges were the same. Summer temperatures at the surface were 15–50°C, at 20 cm 25–32°C and at 60 cm around 25–30°C. Winter temperatures at the surface were 10–30°C, at 20 cm 12–22°C and at 60 cm about 15°C. The slow transfer of heat through the soil caused the maxima and minima to be reached 6 hours after the surface at 20 cm and 12 hours after the surface at 60 cm. After dawn, the surface temperature generally increased sharply until noon, whereafter it would oscillate about the maximum until declining steadily after sunset to a pre-dawn minimum. In the soil, temperatures cycled evenly between daily maxima and minima.

Burrow characteristics and distribution.—Burrows of *S. stirlingi* were unbranched and vertical with somewhat enlarged, horizontal chambers at the base and total lengths ranging from 31–100 cm. Some were slightly spiralled or gently curved. Burrow diameter was constant from top to bottom and there was little silk in the walls. The entrance was circular (diameter 15–27 mm) with a slightly “trampled” flange, but no turret, door or collar of silk. Occasionally, a thin film of silk covered the entrance. Although third instar spiderlings raised in the laboratory constructed small burrows (about 5 mm diameter), none less than 15

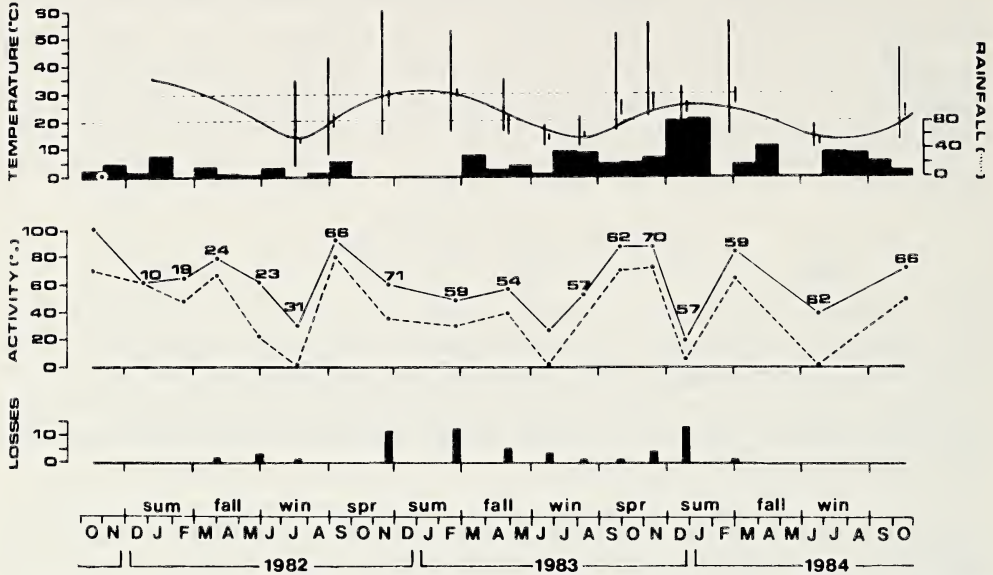


Figure 2.—Environmental conditions and spider activity at Coombah (N.S.W.). Upper: Monthly rainfall totals (solid bars) and diurnal soil temperature ranges: temperatures at 60 cm ($\pm 1^{\circ}\text{C}$ diurnally) (solid line), temperature ranges at the surface and 20 cm (pairs of vertical lines) and the temperature range for spider growth (broken lines) (see text). Middle: Adjusted spider activity (see text); the percentage of open burrows (solid line), burrows in which the occupant was seen (broken line) and adjusted population size (N). Lower: Number of burrows closed for longer than 260 days indicating spiders lost from the population.

mm diameter was found in the field. Therefore the population which was monitored consisted of half to fully-grown spiders.

At the conclusion of the study, the site (approximately 81,000 m^2) contained 111 marked burrows (mean density = 13.7 burrows/ha). Analysis of the number of burrows in each 100 m^2 revealed that the distribution was not random ($\chi^2 = 45.78$, $df = 2$, $p < 0.001$), and that they were clumped ($C.D. = 2.95$) (Sokal & Rohlf 1969) (Fig. 1). Although burrows were scarce near the claypan, no other superficial physical features appeared to be correlated with the distribution of burrows.

There was little correlation between burrow diameter and depth ($r^2 = 0.11$) (Fig. 3). There appeared to be a positive, linear relationship between burrow depth and altitude on the lower slopes (i.e., < 51 m), however, burrow depth appeared to be independent of altitude on the upper slopes (Fig. 4).

Spider activity patterns.—Similar trends of spider activity were observed using two measures: open burrows and those in which spiders were seen at night. Open burrows were those in which spiders were active, or those which were neither plugged by the spider nor closed with sand and debris moved by wind and/or rain, whether the spider was present or absent. Open burrows in which the spiders were not seen may have been recently abandoned, or the spider may have been temporarily out of sight within the burrow. The proportions of spiders seen were generally 10-20% lower than the proportion of open burrows. Activity was low in winter (June-July), peaked in spring (September-November) and early fall (March, April), and was depressed to a variable extent during summer (December-February). Activity data were expected to be unrealistically high in the first 10 months as inactive burrows were generally not found, so only the

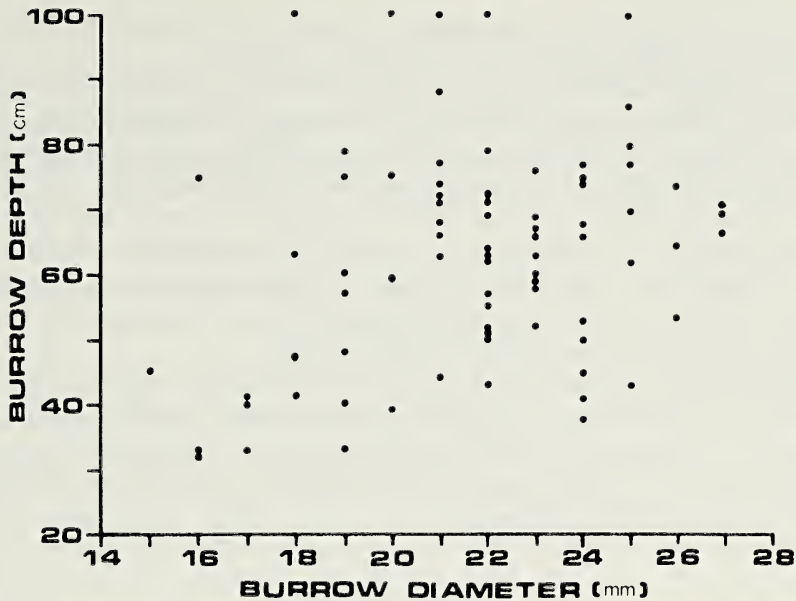


Figure 3.—Relationship between burrow depth and diameter, Coombah (N.S.W. ($N = 80$, $r^2 = 0.11$)).

trends of these data were considered. For the remainder of the study, the absolute percentages of active burrows ranged from 10-85% "open" and 0-75% "seen". As the total number of burrows monitored increased from 72 to 111, the maximum activity levels declined throughout the study to 45% "open" and 35% "seen".

Burrows became blocked from the action of natural agents (such as wind and rain) when the spider did not clear the entrance, or as a result of deliberate plugging by the spider within the top 10-15 cm of the burrow, or both. When

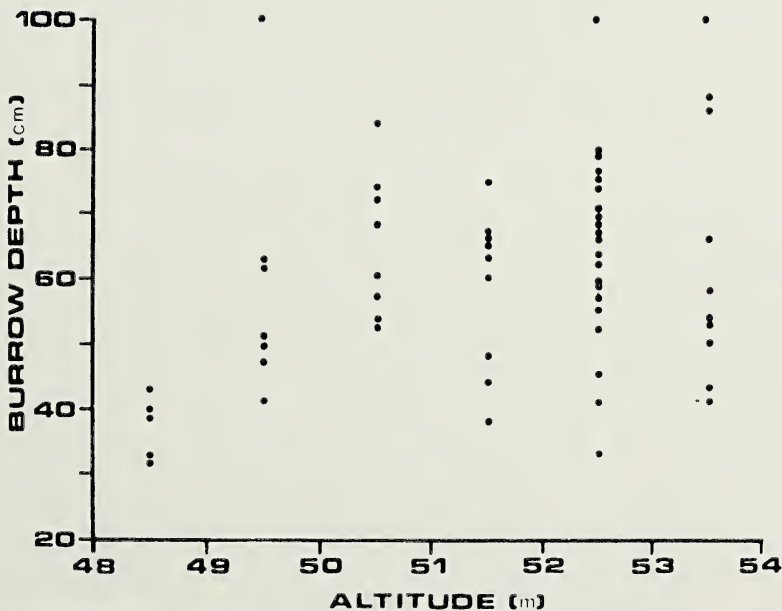


Figure 4.—Relationship between burrow depth and altitude (mid-point between contours), Coombah (New South Wales) ($N = 80$, $r^2 = 0.14$).

burrows were closed, there was usually no evidence of the entrance, and it was generally not possible to determine the cause(s) of closure.

Within 260 days 90.5% of burrows which were inactive became active again. To estimate the losses from the population (from death or dispersal), burrows which remained inactive for periods longer than 260 days were considered to be unoccupied and adjusted activity levels were calculated with the remaining burrows (Fig. 2). While adjusted activity patterns were essentially the same as those obtained with the unadjusted population, the maximum levels were higher at about 90% "open" and 70-80% "seen", in a population ranging from 54-71 burrows. Apparent losses from the population were not uniformly distributed throughout the year, but peaked in summer (Fig. 2).

Small spiderlings (instars II-IV) were seen in December, February and March, indicating egg production in spring and summer. Males usually wandered outside the burrows in March and April (although two were collected as late as June). Together, these observations suggested that molting occurred in late summer and mating from summer through winter.

DISCUSSION

Burrow characteristics.—A high correlation between spider size and burrow diameter has been demonstrated in some burrowing spiders (Decae et al. 1982; Miller & Miller 1984). Petrunkevitch (1911) also suggested that larger spiders should occupy deeper burrows having had longer to dig them. The burrow depth of *S. stirlingi* was independent of burrow diameter (Fig. 3) suggesting that either variable growth was producing different-aged spiders of similar sizes, or that other factors, such as soil moisture or texture, affect burrow depth. The increase in burrow depth with increasing altitude up to 51 m provides circumstantial support for the potential importance of both soil moisture and texture. The formation and maintenance of the sand dunes by the action of wind and water (Bowler 1980) results in the progressive downslope accumulation of clays (Leeper 1964), and potentially an inverse relationship between altitude and soil moisture owing to the water-holding properties of clays. In addition, calcareous layers may form within the dune when the water table recedes (Bowler 1980). Meat ants, *Iridomyrmex purpureus* (Sm.), whose nests are abundant in this area, penetrate these layers as a defense against moisture and thermal stresses and to avoid nest predation (Ettershank 1971). While *S. stirlingi* may use a similar strategy, extensive excavation of burrows would be necessary to clarify this possibility.

Burrow blocking behavior.—The closure of burrows at different times of the year may have different causes. Like other theraphosids, *S. stirlingi* sometimes made burrow plugs by combining sand and web (Gertsch 1949; Minch 1979a). Alternatively, some burrow entrances appeared to become blocked by the natural accumulation of sand and debris as with the wolf spider *Geolycosa wrightii* (Emerton) (Gwynne & Watkiss 1975). Main (1978) and Gray (1968) recorded door-sealing behavior of trapdoor spiders associated with seasonal weather conditions and predator avoidance. For *S. stirlingi*, it seems likely that deliberate plugging was probably most common in summer (providing protection during molting and egg production), while natural weathering may have predominated in winter when spiders were inactive in the cold conditions.

The origin of newly-located burrows is difficult to explain. It seems unlikely that they were new burrows of spiders already in the population or new adult recruits from outside the area as there were never sufficient tailings to indicate excavation of an entirely new burrow. It seems most likely that they were juvenile recruits which had reached sufficient size to be detected (since no burrows smaller than 15 mm were found), and/or existing large burrows which had opened after prolonged periods of closure.

Losses from the population were estimated on the basis of unusually prolonged or continued burrow closure. Spiders may have died due to old age or disease, during molting (as often observed in the laboratory), following attack by parasitic wasps, or they may have dispersed. No evidence was found to suggest that burrows were vacated in favor of new dwellings. However, if spiders dispersed to existing burrows, such activity would still have been recorded as a loss. Molting, mating and production of young in other species of theraphosids are summer activities (Baerg 1958; Minch 1979b), and adult *S. stirlingi* maintained in the laboratory also molted at this time. As the timing of losses coincided with the production of young at Coombah, it seems likely that mid-summer losses may have represented the maturation and departure of males for the following breeding season. Deaths associated with molting would also tend to predominate in summer.

Spider activity.—The potential for growth can be used to relate activity at the burrow entrance with temperatures in the soil. In laboratory studies, rates of growth and development (mediated by food availability) were maximized at 29°C, decreased linearly from 29–25°C and ceased at and below 20°C (Kotzman 1986). At 60 cm within the burrow, 20°C was exceeded only from September through May and 29°C reached only in mid-summer. As the highest levels of activity were recorded consistently in September and October, the spiders probably exploited elevated temperatures near the burrow entrance. Humphreys (1974) recorded almost constant body temperatures in the burrowing wolf spider *Geolycosa goderffroyi* (L. Koch) achieved by behavioral thermoregulation. Similar behavioral adjustment of body temperature in *S. stirlingi* could facilitate feeding, growth and development by allowing the spider to optimize its body temperature for these activities: nocturnal foraging during spring and fall (necessarily near the surface), feeding (anywhere within the burrow), and molting or egg laying in summer (in the chamber at the base of the burrow).

The spring peak of open burrows corresponded to the time when the burrow temperature increased above 20°C and daylength was increasing. Minch (1979b) claimed that temperature was not the cue for burrow unblocking in *Aphonopelma chalcodes* Chamberlin, as spiders at different altitudes (and hence temperatures) opened their burrows at virtually the same time. In addition, he observed that spiders maintained in the laboratory blocked their burrows somewhat later than those in the field, and suggested that photoperiod or temperature might at least moderate the behavior. As both temperature and photoperiod are increasing in spring, it would be difficult to uncouple these factors under field conditions. While it is possible that annual activity patterns may be controlled by an endogenous clock set genetically or during early development (Minch 1979b), it seems more likely that the transition past a temperature limit (Gabel 1972) regulates burrow-blocking behavior through its connection with growth processes.

ACKNOWLEDGMENTS

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LAS ESPECIES DE LA SUBFAMILIA HIPPASINAE DE AMERICA DEL SUR (ARANEAE, LYCOSIDAE)

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ABSTRACT

Nine species of the sixteen that comprise the Hippasinae indicated for South America are studied. *Allocosa brasiliensis* (Petrunkevitch, 1910) n. comb. (= *Moenkhausiana brasiliensis* Petrunkevitch = *Araucaniocosa difficilis* Mello-Leitão n. syn.) is redescribed and the data of the habitat where it occurs is reported. The taxa of *Glieschiella* Mello-Leitão are considered "*species inquirenda*". They should be better placed into *Allocosa*. *Hogna birabenae* (Mello-Leitão, 1941) n. comb. (= *Birabenia birabenae* Mello-Leitão) is not redescribed completely. *Birabenia taeniata* Mello-Leitão, 1943 is considered "*species incerta*" because the holotype is juvenile (it should be a *Tetragonophthalma*, Pisauridae). Although *Sosippus nitidus* (Mello-Leitão, 1944) n. comb. (= *Hippasella nitida* Mello-Leitão) is not redescribed (its holotype is damaged), it is being studied. All taxa are transferred into three subfamilies: Allocosinae, Lycosinae and Sosippinae.

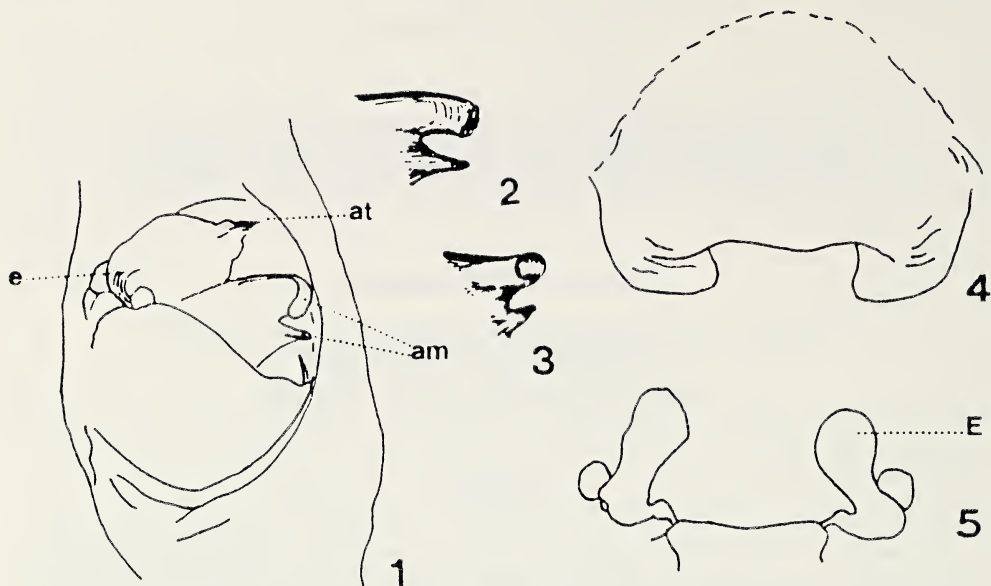
RESUMEN

Se estudian nueve de las dieciseis especies que comprenden las Hippasinae indicadas para América del Sur. Se redescrive *Allocosa brasiliensis* (Petrunkevitch, 1910) n. comb. (= *Moenkhausiana brasiliensis* Petrunkevitch = *Araucaniocosa difficilis* Mello-Leitão n. syn.) y se dan datos sobre el hábitat donde vive. Los taxones de *Glieschiella* son considerados como "*species inquirenda*", y mejor ubicados bajo *Allocosa*. *Hogna birabenae* (Mello-Leitão, 1941) n. comb. (= *Birabenia birabenae* Mello-Leitão) se redescrive fragmentariamente. *Birabenia taeniata* Mello-Leitão, 1943 se considera "*species incerta*", debido a que el holotipo es un ejemplar juvenil (sería una *Tetragonophthalma*, Pisauridae). Se estudia *Sosippus nitidus* (Mello-Leitão, 1944) n. comb. (= *Hippasella nitida* Mello-Leitão) aunque no se describe porque el holotipo está muy deteriorado. Todos los taxones se redistribuyen en tres subfamilias: Allocosinae, Lycosinae y Sosippinae.

INTRODUCCION

Bonnet (1961) enumera para Lycosidae las siguientes subfamilias: Hippasinae Simon, 1898, Pardosinae Simon, 1898, Lycosinae Bertkau, 1878, Cyclocteninae Simon, 1898 y Bradystichinae Simon, 1884. Esta subdivisión fue adoptada, entre otros, por Roewer (1954, 1959, 1960) en cuyos trabajos están indicadas casi todas las Lycosidae de América del Sur.

La subfamilia Hippasinae esté representada en América del Sur por los siguientes taxa: *Porrmosa diversa* (Pickard-Cambridge), *Porrmosa glieschi* (Mello-Leitão), *Porrmosa seccurifera* (Tullgren), *Porrmosa callipoda* (Mello-Leitão), *Porrmosa lagotis* (Holmberg), *Porrmosa harknessi* (Chamberlin),



Figuras 1-5.—*Allocosa brasiliensis* (Petrunkévitch); 1, tarso del palpo izquierdo del macho, ventral; 2, apófisis mediana (*A. difficilis* Mello-Leitão, tipo, MNRJ, Chile, Maullín); 3, apófisis mediana (*M. brasiliensis* Petrunkévitch, lectotipo, PMNH, Brasil, Ypiranga); 4, epigino, ventral; 5, espermatecas (MHNM, Uruguay, Marindia).

Porrmosa castanea (Mello-Leitão), *Hippasella nitida* Mello-Leitão, *Birabenia birabenae* Mello-Leitão, *Birabenia taeniata* Mello-Leitão, *Moenkhausiana brasiliensis* Petrunkévitch, *Moenkhausiana argentinensis* Mello-Leitão, *Glieschiella halophila* Mello-Leitão, *Glieschiella senex* Mello-Leitão, *Glieschiella alticeps* Mello-Leitão, *Araucaniocosa difficilis* Mello-Leitão.

Dondale (1986) definió Lycosidae sobre la base de tres sinapomorfías: (a) ojos dispuestos de manera peculiar, (b) tibia del palpo en los machos sin apófisis retrolateral y (c) madres que transportan activamente las ootecas en las hileras y las arañitas jóvenes sobre su abdomen. Asimismo subdividió la mencionada familia también en cinco subfamilias: Sosippinae Dondale, 1986, Venoniinae Lehtinen e Hippa, 1979, Allocosinae Dondale, 1986, Pardosinae Simon, 1898 y Lycosinae Simon, 1898.

En el sistema de este autor, obviamente, se cambian las denominaciones, pero además la agrupación de los géneros es diferente a la de Roewer. La esencia de la diferencia se halla en que, Roewer, desestimó el valor diagnóstico del cymbium y del epigino, mientras que Dondale se basó en la morfología de los órganos genitales. Hoy, prácticamente, existe consenso entre los especialistas de la familia sobre que, la clasificación de Roewer, está apoyada en criterios que no responden totalmente a la realidad. (En efecto, no pude comprobar, en el examen de un número significativo de tipos de especies de América del Sur, la constancia de los caracteres genéricos usados por Roewer. La mayoría de las especies revisadas por mí, las cuales dicho autor ubicó en los géneros redefinidos por él, no "entraron" en esos géneros).

Ante esta situación consideré conveniente adecuar las Lycosidae de esta parte del Continente, a los conceptos de Dondale. La finalidad de mi proyecto fue, en una primera etapa, integrar las especies de Hippasinae de América del Sur a una clasificación sistemática más objetiva que la de Roewer.

Este artículo informa los resultados de esa investigación, la cual reubica los miembros de Hippasinae de América del Sur en 3 subfamilias, según fueron definidas por Dondale (1986).

Métodos de presentación.—Abreviaturas: MLP, Museo de La Plata, Argentina; MNRJ, Museu Nacional de Rio de Janeiro, Brasil; CAS, California Academy of Sciences, San Francisco, USA; MZUC, Museo de Zoología, Universidad de Concepción, Chile; PMNH, Peabody Museum of Natural History, Yale University, USA; MRCN, Museu Riograndense de Ciencias Naturais, Porto Alegre, Brasil; MNHM, Museo de Historia Natural de Montevideo, Uruguay; a, atrium am, apófisis mediana; amt, apófisis mesial del tegulum; at, apófisis terminal; c, conductor; E, espermateca; e, émbolo; t, tegulum.

Los valores merísticos están dados en milímetros, significando: extremos; media \pm desviación típica (ejemplares medidos).

Salvo indicación, las descripciones están basadas en más de 10 ejemplares conservados en alcohol.

Subfamilia Allocosinae

Allocosa brasiliensis (Petrunkevitch, 1910) nueva combinación Figuras 1-7, Mapas 1-2

Moenkhausiana brasiliensis Petrunkevitch, 1910: 223, figs. 26-29; 1911: 569; Bonnet, 1957: 2971.

Araucaniocosa difficilis Mello-Leitão, 1951:328, fig. 1; Casanueva, 1980: 22, figs. 17-19 (in part, identificación errónea); Brignoli, 1983: 438. Sinónimo nuevo.

Glieschiella sp.: Capocasale, 1982: 3.

Glieschiella halophila: Dondale, 1986: 331.

Diagnosis.—Especie distribuida en el Sur de América del Sur. Habita espacios abiertos, suelos arenosos y costas de ríos y lagunas. Hace agujeros en el suelo que recubre interiormente con tela. La coloración general del cuerpo es amarillo muy pálido (mimetiza con la arena). Los machos tienen la “palea” muy desarrollada, la apófisis mediana del palpo es bífida, una rama es puntiaguda la otra roma, curvada y canaliculada. Las hembras carecen de “septum” mediano y de “atrium”, las espermatecas son bulbosas y sin nódulo. La longitud corporal en ambos sexos cubre extremos entre 11-20 mm.

Descripción.—*Macho*: Cuerpo: largo total 11.9-19.6; 14.24 ± 4.67 (13); cefalotórax: largo 6.0-9.8; 8.05 ± 1.00 (13); ancho: 5.0-8.1; 6.14 ± 1.00 (13); castaño-amarillo; área ocular: castaño-rojo manchada de castaño oscuro; márgenes: castaño-oscuro. Esternón: castaño-rojo (en algunos ejemplares amarillo pálido). Quelíceros: castaño-rojo. Patas: fémures: I, 4.7—8.5; 6.48 ± 1.14 (13); II, 4.3—7.7; 6.09 ± 0.96 (13); III, 4.0—8.2; 5.97 ± 1.07 (13); IV, 5.0—9.8; 7.25 ± 1.39 (13); amarillos; basitarsos: castaño-rojo. Abdomen: amarillo pálido con manchas negras dorsalmente; puntuaciones negro lateralmente; amarillo pálido ventralmente. Palpos: “cymbium” con una apófisis mediana bífida, una rama corta y puntiaguda la otra curvada ventralmente canaliculada (Figs. 2, 3); “palea” desarrollada; apófisis terminal corta, aguda, poco visible.

Hembra: Cuerpo: largo total 11.2—14.7; 13.41 ± 1.38 (14); cefalotórax: largo 6.0—8.0; 6.81 ± 0.95 (14); ancho 4.6—7.1; 5.26 ± 0.87 (14). Fémures: I, 4.1-7.2; 5.71 ± 0.85 (14); II, 4.0—6.3; 5.28 ± 0.86 (14); III, 3.7—6.5; 5.37 ± 0.87 (14); IV, 4.4—8.6; 6.59 ± 1.10 (14).



Figura 6.—Marindia (Uruguay) hábitat de *Allocosa brasiliensis* (Petrunkévitch). Las flechas indican los lugares donde generalmente se encuentra la especie.

La hembra cromáticamente es muy semejante al macho. Epigino: sin “septum” ni “atrium”; espermatecas bulbosas, sin nódulos; tubos copulatorios cortos (Figs. 4, 5).

Distribución.—(Maps. 1, 2) Sur del Brasil, Sur-Oeste de Uruguay y centro de Chile.

Hábitat.—Espacios abiertos y suelos arenosos de las costas de ríos y lagunas. Este hábitat tiene amplias variaciones de temperatura durante el día debido a que la vegetación es escasa y prácticamente no hay sombra (Fig. 6).



Figura 7.—Agujeros hechos por un ejemplar inmaduro de *Allocosa brasiliensis* (Petrunkévitch). La fotografía muestra la estructura de los agujeros los cuales tienen 2 entradas cerradas; ambos agujeros se comunican.



Mapas 1, 2.—1, Distribución conocida de *Allocosa brasiliensis* (Petrunkevitch); 2, Sector de América del Sur indicado en el mapa 1.

El porcentaje de humedad relative es alto por la proximidad de las fuentes de agua, la velocidad de las corrientes de aire es baja a nivel del suelo. Cuantitativamente el componente biológico predominante son las hormigas.

Desde el punto de vista ecológico, este hábitat correspondería a lo que Elton y Miller (1954) denominaron como: "Aquatic-terrestrial system".

Un lugar físico en el cual se resumen las características estructurales del hábitat (donde es muy frecuente hallar a *A. brasiliensis*) es El Pinar (Uruguay). Se dan a continuación los datos de los factores bióticos y abióticos obtenidos en dicho lugar, en noviembre (1988) (época de alta actividad de la especie) a las 1900 horas ("instante climatológico medio"): Vegetación herbácea predominante: *Senecio* sp. y *Panicum* sp. Mesofauna a nivel del suelo: *Tetragonoderus* sp. (Coleoptera) *Tronistes* sp. (Coleoptera), *Labidura* sp. (Dermaptera), *Acromyrmex* sp. (Hymenoptera), *Liolaemus* sp. (Lacertilia, Iguanidae). Temperature (grados Celsius): a m. 0.10 por debajo del suelo, 22.6°, a nivel del suelo, 19.10°, a m.1 sobre el suelo, 19.4°; Humedad Relativa: a nivel del suelo, 98%, a m.1 sobre el suelo, 96%. Velocidad de las corrientes de aire (millas por hora): a nivel del suelo 3, a m.1 sobre el suelo, 11.

Agujeros.—Los adultos de *A. brasiliensis* cavan bajo la superficie del suelo, agujeros más o menos verticales, que recubren interiormente de tela, de una profundidad que puede llegar a los 10 cm. Algunas veces se puede ver, en estudios experimentales, que ejemplares inmaduros cavan agujeros de 3 a 6 cms, con 2 entradas cerradas cuyas 2 ramas convergen en un agujero simple (Fig. 7).

Comportamiento constructor de refugios.—El comportamiento constructor de refugios, es esencial en el cavado de agujeros; es muy estereotipado. Para su estudio y considerando el tema con extrema sencillez, puede ser desintegrado en 6 unidades comportamentales: búsqueda; giro de 90 grados; cavado/toma de piedras; depósito; sellado; giro de 180 grados.

Las partes anatómicas que la araña utiliza en cada unidad de comportamiento son: en la de búsqueda las patas I y II; en la de cavado/toma de piedras los quelíceros y pedipalpos; en la de sellado las hileras.

Comentarios.—Del análisis del "cymbium" del tipo de *Araucaniocosa difficilis* concluí que es coespecífico con el lectotipo de *Moenkhausiana brasiliensis*. La apófisis mediana y la apófisis terminal son semejantes en los tipos de ambas especies. La cantidad de dientes internos en los quelíceros y las medidas del área

ocular también son semejantes. Por supuesto, como *M. brasiliensis* es un ejemplar joven existen diferencias en el tamaño. Como regla general podría establecerse que, cuanto mayor es un ejemplar, la apófisis mediana más se parece al esquema de la figure 2.

El análisis de dichos caracteres agregado a los datos ecológicos disponibles me condujo a la conclusión que, *Moenkhausiana* y *Araucaniocosa* son sinónimos recientes ("junior synonyms") de *Allocosa*.

Roewer (1954, 1959) y Brignoli (1983) indicaron 14 especies de *Allocosa* para América del Sur. Yo no estimo que todas esas especies puedan ser ubicadas allí aplicando el concepto actual de este género, (por ejemplo ni *Allocosa mutillata* (Mello-Leitão) ni *Allocosa paraguayensis* (Roewer) pertenecen a dicho género). De acuerdo con la lectura de las descripciones específicas, establecí como hipótesis de trabajo que, *Allocosa* podría ser dividido formalmente en 2 grupos: el grupo *Allocosa funerea* y el grupo *Allocosa brasiliensis*. Pero antes de sacar conclusiones, será necesario revisar cada uno de los tipos de las especies para fundamentar factualmente los grupos mencionados. (Esta carencia hizo que me abstenga de hacer una diagnosis diferencial para *A. brasiliensis*).

Si se analiza la figure 18 del artículo de Casanueva (1980) se comprueba que fue cometido un error. Ni el epigino ni las espermatecas son como en *A. difficilis*. Al examinar los ejemplares estudiados por Casanueva (1980) concluí que pertenecen a una Lycosinae. De acuerdo con el nivel actual de mis conocimientos en la familia no la pude identificar aun.

Los datos ecológicos obtenidos en el hábitat tienen significación sistemática. Estoy de acuerdo con Brady (1979: 174) quien juzga que esta clase de información es tan útil al sistemático como la relacionada con las características morfológicas. En el hábitat donde se halla *A. brasiliensis* hay ausencia total de arañas de otras familias. Por tal razón, estimo que la estructura de ese ecosistema es un carácter diagnóstico importante que debe usarse también desde el punto de vista sistemático.

Ejemplares examinados.—Veinte ejemplares identificados por Casanueva como *A. difficilis* de CHILE: Temuco, 20 km E Temuco, 7 Ene. 51 (Ross, Michaelbacher), 4 hembras, 2 machos, 3 juveniles (CAS), identificación errónea; Temuco, 25 km E Temuco, invierno 51 (M. Smith), 1 juvenil (CAS); Bio Bio, Negrete, 29 Ene. 51 (Ross, Michaelbacher), 8 juveniles (CAS); Osorno, 20 km E. Puyehue, 26 Ene. 51 (Ross, Michaelbacher) 1 macho (CAS), identificación errónea; Lapihue, sea coast of P. Montt, 21 Ene. 51 (Ross, Michaelbacher) 1 hembra (MZUC). Un ejemplar identificado por Mello-Leitão, Maullín, 1 macho (MNRJ) tipo. Un ejemplar identificado por Petrunkevitch como *Moenkhaausiana brasiliensis* de BRAZIL: Ypiranga (Moenkhause), 1 macho (PMNH) lectotipo, sensu Lise. Ochenta y dos ejemplares identificados por el autor de URUGUAY: Montevideo, Pajas Blancas, 27 Ene. 1980 (Gudynas), 1 macho (MHNM); Paysandú, 11 Oct. 1976 (Capocasale, Bruno), 2 hembras, 2 machos (CAS); Canelones, Marindia, 8 Abr. 1976 (Capocasale, Costa), 15 hembras, 15 machos (MHNM); Canelones, Marindia, 8 Dic. 1975 (Costa, Urruty), 2 machos, 1 inmaduro (CAS); Canelones, Las Toscas, 2 Mar. 1941 (Robayna), 2 hembras (MHNM); Soriano, Santo Domingo, 19 Ene. 1977 (Bonino), 1 hembra (MHNM); Soriano, Isla Pepe Ladrón, 17 Ene. 1977 (De Sá), 1 macho (MHNM); Río Negro, Isla Barrientos. Feb. 1977 (Olazarri), 1 hembra, 1 macho (MHNM); Colonia, Nueva Palmira, 6 Dic. 1970 (Capocasale), 2 machos, 5 inmaduros (CAS); Colonia, Punta Gorda, 26 Feb. 1968 (Capocasale, Bruno), 1 hembra, 1 inmaduro (MHNM); Colonia, Playa de la Agraciada, 6 Set. 1958 (Bonino), 1 macho (MHNM); Rocha, Laguna Negra, 16 Feb. 1976 (Blengini), 1 hembra (MHNM); Rocha, Cabo Polonio, Feb. 1976 (Capocasale), 1 macho (CAS); Rocha, Parque Santa Teresa, Dic. 1977 (Costa), 10 hembras, 6 machos, 2 juveniles (MHNM); San José, San Gregorio, 4 Set. 1966 (Morey), 1 hembra (MHNM) Maldonado, Laguna del Sauce, 29 Ago. 1976 (Costa, Urruty), 1 hembra, 3 machos (MHNM); Maldonado, Punta Colorado, 8 Feb. 1978 (Aleman), 2 machos (MHNM); Maldonado, ruta 10, Km 112, 25 Dic. 1975 (Capocasale), 1 macho (CAS).

Species incerta.—*Moenkhausiana argentinensis* Mello-Leitão, 1938:99, f. 14. Un ejemplar de Argentina: Río Negro, Isla Tehuel Malal (tipo inmaduro) examinado, depositado en el MLP.

Glieschiella Mello-Leitão

Species inquirenda.—Como actualmente solo examiné 2 de los 3 tipos de este género, solo tengo los siguientes comentarios respecto de sus miembros.

Glieschiella alticeps Mello-Leitão, 1944: 347, f. 37-38. Dos ejemplares de Argentina, San Blás (sintipos, 1 macho; 1 hembra, inmaduros) examinados, depositados en el MLP. En el MNRJ hay 2 ejemplares adultos (paratipos, 1 macho; 1 hembra) examinados, sobre la base de los cuales, seguramente, Mello-Leitão hizo su descripción. (Considero esta especie válida).

Glieschiella halophila Mello-Leitão, 1932: 69; 1943 a: 161, f. 19. (No hallé el tipo de esta especie que estaría depositado en el MNRJ. El Dr. A. Lise me informó (com. pers.) que es un ejemplar inmaduro. Dondale (1986) señaló: “*Moenkhausiana* (type: *Moenkhausiana brasiliensis* Petrunkevitch, 1910). . . the generic name is a senior synonym of *Glieschiella* Mello-Leitão, 1932 (type: *Glieschiella halophila* Mello-Leitão, 1932)”. (No discuto esa conclusión. De acuerdo con ésta y según la sinonimia anotada anteriormente por mí, todas las especies de *Glieschiella* pasarían al género *Allocosa*).

Glieschiella senex Mello-Leitão, 1945: 254. Un ejemplar de Argentina, Entre Ríos, Colón. (tipo, hembra) examinado, muy deteriorado, depositado en el MLP. (El examen del “cymbium”, que pude recuperar a pesar del estado del ejemplar, confirmaría mi hipótesis que pertenece a *Allocosa*. Considero esta especie sinónima).

Subfamilia Lycosinae

Hogna birabenae (Mello-Leitão, 1941) nueva combinación Figuras 8-11

Birabenia birabenae Mello-Leitão, 1941: 137, figs. 27, 33, 34; Roewer, 1954: 310; 1960: 1005, Brignoli, 1983: 432.

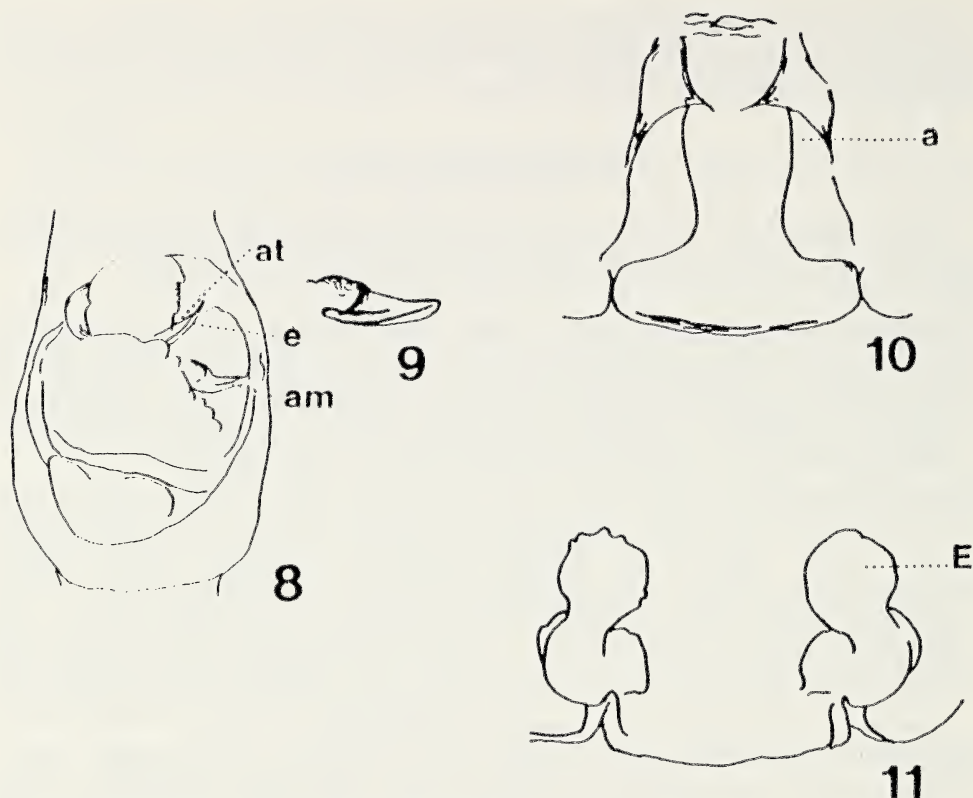
Diagnosis.—Es poco práctico, dado el estado en que están los ejemplares, dar una diagnosis de esta especie basándose en la observación de los 4 ejemplares útiles, actualmente disponibles.

Descripción.—(ver Comentarios). *Macho*: Cuerpo: largo total 11.3 (1); cefalotórax: largo 5.4 (1); ancho 4.3 (1). Palpos como en las figuras 8 y 9.

Hembra: Cuerpo: largo total 9.7—12.3 (2); cefalotórax: largo 4.5—5.6 (2); ancho 3.2—3.8 (3). Epigino y espermatecas como en las figuras 10 y 11. (Otros caracteres ver Mello-Leitão, 1941: 137).

Distribución.—Norte y centro de la República Argentina.

Comentarios.—En el Museo de La Plata están depositados los únicos cinco ejemplares (tipos) disponibles (un macho, tres hembras, adultos, una hembra inmadura). Todos están muy deteriorados; los miembros, el cefalotórax y el



Figuras 8-11.—*Hogna birabene* (Mello-Leitão); 8, tarso del palpo izquierdo del macho, ventral; 9, apófisis mediana (*B. birabene* Mello-Leitão, alotipo, MLP, Argentina, Tucumán); 10, epigino, ventral; 11, espermatecas (*B. birabene* Mello-Leitão, tipo, MLP, Argentina, La Rioja).

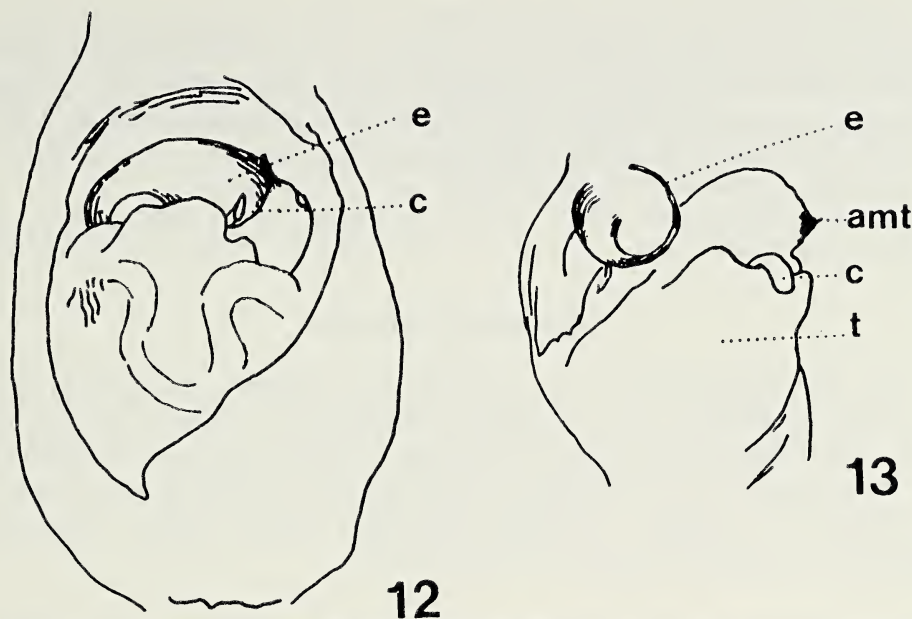
abdomen se hallan separados. A pesar de lo anterior es posible ubicar genéricamente la especie basándose en el examen de la genitalia, el cual permite concluir que pertenece al género *Hogna*.

El lamentable estado en que están los tipos y paratipos de esta especie, inhibe hacer una redescrición satisfactoria. El procedimiento para identificar la especie, que solucionaría esta deficiencia, sería consultar la descripción de Mello-Leitão (1941: 137) completándola con los datos y figuras dados en este trabajo.

Las diagnósis de Mello-Leitão (1941) y de Roewer (1959) no coinciden con las conclusiones que se sacan luego de examinar los tipos. De acuerdo con esas conclusiones y luego de considerar todos los géneros de Lycosinae establecidos por Roewer, se estaría ante un género nuevo. Yo preferí no seguir esa línea de razonamiento por las razones expuestas en la Introducción.

Ejemplares examinados.—Cinco ejemplares identificados por Mello-Leitão como *Birabenia birabene* de ARGENTINA: Tucumán, Bañado (Birabén), 1 macho (MLP) alotipo; La Rioja, Sañogasta (Birabén), 2 hembras, 1 hembra inmadura (MLP); Santa Fe, Vera, 1 hembra (MLP).

Species incerta.—*Birabenia taeniata* Mello-Leitão, 1943: 108, fig. 9. Un ejemplar de Argentina, Córdoba, Bell Ville (tipo, inmaduro) examinado, depositado en el MLP. (El examen de los dientes internos de los quelíceros y de los ojos dio que se podría tratar de una especie de *Tetragonophthalma*—Pisauridae—).



Figuras 12, 13.—*Sosippus nitidus* (Mello-Leitão) tarso del palpo izquierdo del macho; 12, ventral; 13, lateral externa (*S. nitidus* Mello-Leitão, tipo, MLP, Argentina, La Plata).

Subfamilia Sosippinae

Porrimosa Roewer

Comentarios.—Las conclusiones sobre las especies del género *Porrimosa* fueron tratadas en un artículo anterior (Capocasale 1982); se pueden resumir en dos grupos:

Especies incerta.—*Porrimosa diversa* (Pickard-Cambridge) (tipo inmaduro), *Porrimosa glieschi* (Mello-Leitão) (tipo inmaduro), *Porrimosa securifera* (Tullgren) (tipo inmaduro), *Porrimosa callipoda* (especie descrita incompletamente; tipo perdido).

Especies seguras.—*Porrimosa lagotis* (Holmberg), *Porrimosa harknessi* (Chamberlin) (descrito solo el macho), *Porrimosa castanea* (Mello-Leitão) (descrita solo la hembra).

Sosippus nitidus (Mello-Leitão, 1944) nueva combinación

Figuras 12-13

Hippasella nitida Mello-Leitão, 1944: 343, fig. 32; Roewer, 1954: 313.

Comentarios.—Hoy, el único ejemplar disponible, en colección es el tipo y está considerablemente deteriorado. Es imposible ubicar las patas y otras partes del cuerpo, dado que están separadas, excepto un trozo del ceralotórax y un pedipalpo. Son las únicas partes rescatables. Esto me inhibe de diagnosticar género y especie, así como redescubrir la última.

No obstante, a pesar del pésimo estado de conservación de este ejemplar, el examen del trozo del cefalotórax que contiene el 70% aproximadamente del área ocular, indicó que es similar a la diagnosis que dio Brady (1962) para *Sosippus*. Asimismo el tarso del pedipalpo carece de "palea" y de apófisis terminal. Todo lo cual lleva a concluir que, este ejemplar, pertenece a *Sosippus*.

Hippasella, por lo tanto, es un sinónimo nuevo de *Sosippus*.

Ejemplares examinados.—Un ejemplar identificado por Mello-Leitão de ARGENTINA: La Plata (Birabén), 1 macho (MLP) tipo.

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INCORPORATION OF URTICATING HAIRS INTO SILK: A NOVEL DEFENSE MECHANISM IN TWO NEOTROPICAL TARANTULAS (ARANEAE, THERAPHOSIDAE)

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ABSTRACT

Two species of New World theraphosid; *Theraphosa leblondi* from French Guiana, and *Megaphobema* sp. from Ecuador incorporate abdominal setae into silk constructs. *Theraphosa* incorporates setae into the egg sacs and the silk mats on which they molt. *Megaphobema* sp. includes them in the egg sacs only. The setae used in the egg sacs by both these spiders are from the lateral region of the abdomens, the setae which *Theraphosa* uses in the silk mat are from the lateral and posterior regions. All abdominal regions tested on *Theraphosa* had urticating hairs present. To test the possible benefits of this behavior, the egg sacs and silk mats were tested for urticarial effect. The egg sacs failed to elicit any urticarial response in either humans or two species of mouse (*Mus musculus* and *Peromyscus* sp.). Egg sac material with or without setae was found to be an effective barrier to the larvae of the fly *Megaselia scalaris*. The silk mats of *T. leblondi* were found to be more effective at stopping the movement of *M. scalaris* larvae than theraphosid silk which lacked them.

INTRODUCTION

Urticating setae have been well documented in both the larval and adult instars of lepidopterous insects, particularly those in the family Saturniidae. The urticating setae of the Lepidoptera are known to employ either a chemical urticant, mechanical irritation, or both (Goldman et al 1960; Pesce and Delgado 1971). Mygalomorph spiders in the family Theraphosidae have also been known to possess urticarial setae (Bates 1836), but only recently has the phenomenon been examined (Cooke et al. 1972; Cooke et al. 1973).

Cooke et al. (1972) examined specimens in museum collections and described four basic urticating hair types in New World theraphosids (Old World tarantulas apparently lack them). In contrast to the urticating setae of the Lepidoptera, the urticating hairs of tarantulas rely on mechanical irritation alone. These setae are characterized by a penetrating end (which may be at the proximal or distal end), with fine barbs located along the point and longer barbs along the shaft. The base of the hair has a constriction which serves as a break-off point. Tarantula

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defensive hairs are concentrated on the posterior region of the abdomen, although there is an exception to this in the genus *Epebopus* (Marshall and Uetz 1990). Most tarantulas possess a suite of behaviors which accompany defensive hair shedding. These may be stridulating, rearing and striking with the first two pairs of legs, and attempting to bite. The hairs are shed by rapid downward strokes of one or both of the fourth legs with the ventral surface of the tibia being applied to the posterior abdomen.

Two tarantula species; *Theraphosa leblondi* Latreille (1804) from French Guiana, and *Megaphobema* sp. Pocock (1901) from Ecuador (adult male and female specimens have been deposited in the collection of the Queensland Museum, Brisbane, Australia) have been observed to incorporate lateral abdominal setae into their egg sacs. Additionally, captive *Theraphosa* have been observed to shed hairs onto the silk mat upon which they molt. The phenomenon of incorporating urticating hairs into silk constructs has also been noted for *Avicularia* sp. in Trinidad, which apparently include the hairs in their retreats for defense against predators (A. Bordes in Cooke et al. 1972). In this study we investigate the defensive use of urticarial hairs by *Theraphosa*; their distribution on the abdomen, and their incorporation into shedding mats and egg sacs.

METHODS

Specimens of *Theraphosa* and their egg sacs were collected in the field in French Guiana between 1981 and 1988, and egg sacs were also collected from the laboratory colony. The specimens of *Megaphobema* were collected in the vicinity of Puerto Misuali, Ecuador in December of 1984. The shedding mats were collected from the cages of recently molted *Theraphosa* and stored for later use. *Megaphobema* has not been observed to make such mats.

To investigate the range of distribution of urticating hairs on the abdomen of *Theraphosa*, a comparative survey of hairs on three regions (lateral, dorsal, and posterior) of the abdomens of five preserved specimens was made. The lateral area was chosen as it was the region from which the hairs were shed for the egg sac, the dorsal area because it is a region not known to be associated with any hair shedding behavior, and the posterior area as it is the site of the hairs used in defense. A 1.0 mm square sample of cuticle was dissected out of each site from each specimen and the hairs were scraped off onto a microscope slide and dispersed in a drop of mounting medium by stirring with a probe. Four regularly spaces, parallel transects were taken across the slide and all the hairs were counted and classified as urticating or non-urticating.

The pubescence of the egg sacs of both *Theraphosa* and *Megaphobema* is obvious to the unaided eye. Scanning electron micrographs were prepared of *Theraphosa* egg sac material for closer examination of the structure of the silk-hair matrix. To examine the composition of hairs in the egg sac material, 1.0 mm square samples were taken from five egg sacs. The silk-hair matrix was teased apart, mounted on a slide and the two hair types counted in total. The inclusion of hairs into the shedding mats was measured by taking a 2.0 mm square sample from five shedding mats produced by captives. The material was shredded and dispersed in mounting medium as with the egg sacs. The hairs were counted and classified in total.

To test the urticarial action of the egg sac material against predators, studies were conducted on three vertebrate species, and one invertebrate species. The effect of the egg sac material on humans was tested by rubbing an egg sac against the underside of the forearms of three human volunteers. This was seen as adequate, since the human response to the defensive shedding of posterior abdominal hair by *Theraphosa* is immediate and strong. The shed hairs are borne up on air currents, resulting in a burning, itching sensation on exposed skin surfaces and in the upper respiratory tract. In a test of the egg sac material's effect on a small vertebrate predator model, six wild-caught deer mice (*Peromyscus* sp.) were used. A sample of egg sac material was applied to the mouths of restrained individuals by holding a piece in a forceps and rubbing it around the mouth-nose area, after which the mouse was returned to its cage and observed for fifteen minutes. In both these tests, any inflammation or behavioral evidence of itching was considered a positive response.

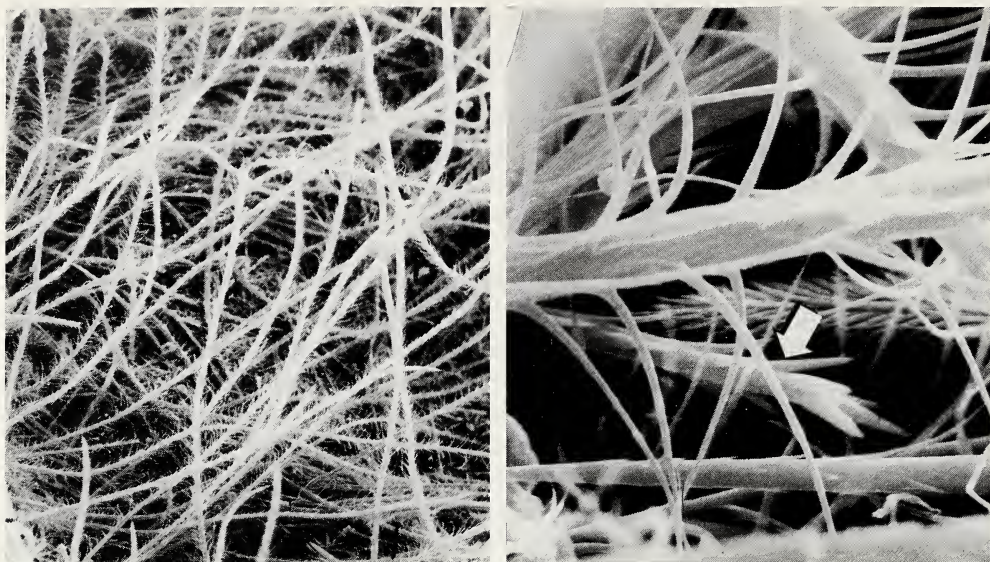
To test for the effect of ingesting hairs, a 1.0 cm square sample of egg sac material was shredded and incorporated into 30.0 gm of peanut butter and offered to the deer mice. A second test was performed to examine the effectiveness of intact egg sac material in deterring vertebrate predation. Samples of material from *Theraphosa* egg sacs were used to enclose the ends of two 10.0 cm by 3.5 cm cylindrical plastic vials that were baited with peanut butter. White laboratory mice (*Mus musculus*) were used. The mice were tested in two groups of five. First, they were fed peanut butter to accustom them to the smell and taste, and then they were fasted for six hours, having free access to water, after which they were offered the tubes (one to a group).

A phorid fly occurs in association with *Theraphosa* in French Guiana (Marshall, pers. obs.). This species belongs to the genus *Megaselia*, and is undescribed (W. H. Robinson pers. comm.). Adult flies have been observed on the spiders in both the field and captivity; the late instar larvae are seen on the cephalothorax and femora, and puparia were found affixed to the cephalothoracic apodeme and the femora. As this fly is the only known parasite of *Theraphosa* (other than an unidentified mite) a congeneric phorid (*Megaselia scalaris*) was selected to test the deterrent effect of the silk-hair constructs. The flies were trapped from a laboratory cricket colony. *M. scalaris* is a common scavenger, and freely oviposits on dead animal material. Material from two field collected *Theraphosa* and one captive-produced *Brachypelma smithii* Simon (1891) egg sac was used to enclose the ends of patent-lip vials baited with dead crickets. *Brachypelma* was used as it does not include hairs in the egg sac. One vial capped with fine nylon mesh was used as a control. These seven vials were placed in a cage with approximately 60 flies.

The shedding mats were also tested using larval *Megaselia scalaris*. The ability of these larvae to move about on the shedding mats was compared to the total distance travelled on non-pubescent silk matting laid down by captive *Avicularia* sp. from French Guiana (this silk had been examined for setae and none were found). The trials were run for 10 minutes.

RESULTS

Both field-collected and captive-produced *Theraphosa* egg sacs are pubescent in



Figures 1, 2.—SEM of *Theraphosa* egg sac material: 1, the outer covering of hair; 2, a close-up with a Type III urticating hair indicated by the arrow.

appearance. The scanning electron micrographs revealed that the egg sac material is covered with a mixture of the long, non-urticarious body hairs and the smaller urticarious hairs (Figs. 1, 2). The much larger non-urticarious hairs are the most obvious, despite the numerical dominance of the urticating hairs. In the process of making the egg sac, the female *Megaphobema* and *Theraphosa* denude the lateral regions of their abdomen (Figs. 3, 4). This behavior is in contrast to the shedding of posterior abdominal hairs during defensive displays. While *Megaphobema* egg sacs were not microscopically examined, a captive specimen of *Megaphobema* was observed in the process of producing an egg sac. The female begin by laying down a circular mat of silk within the retreat by standing in the center and turning around. The spider would then pause and shed the hairs with slow, downward stroking motions of the fourth tarsal scopula against the lateral areas of the abdomen. Alternate sides were used between bouts of hair shedding. The behavior is similar to preening in both tempo and use of the tarsal scopulae.



Figures 3, 4.—*Megaphobema* sp. females before (3), and after (4) production of an egg sac. The denuded lateral regions of the abdomen are visible in 4, indicated by an arrow.

Table 1.—Two-way ANOVA on the proportion of urticating hairs on the dorsal, lateral, and posterior abdominal regions of five females of *Theraphosa leblondi*.

	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i> ratio	<i>P</i>
Regions	1669.91	2	834.96	25.47	$P < 0.005$
Specimens	296.62	4	74.16	2.62	$P > 0.1$
Error	262.24	8	32.78		
Total	2228.77				

While egg-laying behavior has never been observed in *Theraphosa*, it is assumed to be the same.

In the samples taken from *Theraphosa* abdomens, urticating setae were found at all sites sampled, and were the numerically dominant type. The percent urticating hairs among the setae on the dorsal region of the abdomen was 87.0 ± 3.0 (mean \pm one standard deviation); the lateral 74.0 ± 0.06 ; and the posterior 95.0 ± 7.0 . The urticating hairs were all what Cooke et al. (1972) refer to as type III (V. Roth, pers. comm.). The urticating hairs from the posterior abdomen were longer, ranging from 0.5-1.0 mm. In the other two sites sampled, the hairs were approximately 0.1 mm.

A two-way ANOVA testing variation between sites and between spiders was performed using the arc-sine transformed proportion of urticating hairs. The difference between the sites was significant, but not between spiders (Table 1). When the proportion of urticarial hairs in the egg sac material and the lateral abdomen were compared using a Mann-Whitney *U* test, the results were not significantly different. The five egg sacs had 66.0 ± 2.0 percent urticating hairs. In the five shedding mats both the long posterior and short lateral urticating hairs were mixed, and together comprised 86.0 ± 4.0 of the total hairs. Taken separately, the long urticating hairs constituted 24.0 ± 14.0 , and the short urticating hairs were 63.0 ± 17.0 .

In the tests for an urticarial response to egg sacs applied to the skin, no itching was reported by the human volunteers. Mice did not appear distressed nor did they indulge in excessive grooming behavior after similar exposure.

In the first feeding test, all the peanut butter-egg sac material mixture was consumed. Microscopic examination of the feces revealed both urticating and non-urticating hairs had been ingested and passed through, and the mice appeared normal. In the second feeding test, using intact material, the results were similar. The mice initially investigated the tubes, sniffing and nibbling at the material, and then ignored them. The tubes were left in the cages overnight, and 15 hours later, the egg sac material had been chewed and partially consumed, along with a portion of the peanut butter. There were no egg sac fragments in the cage, and it was mostly gone from the tubes. Examination of the feces once again revealed that the hairs (and silk) had been ingested and passed through without adverse effects.

The phorid experiment was terminated after 72 hours when the adult flies were dead. The flies had oviposited on the control vial (with the mesh on top), one *Brachypelma* vial and one *Theraphosa* vial. Larvae were observed in the control vial only. The *Theraphosa* shedding mats were more effective at slowing the progress of the phorid larvae (mean distance in mm travelled in 10 minutes \pm one standard deviation: *Theraphosa* mats, 8.8 ± 6.8 ; *Avicularia* webbing, 42.0 ± 33.5 ;

$t = 2.17$, $df = 8$, $p = 0.06$). All the phorid larvae on the *Theraphosa* webbing eventually stopped. On the *Avicularia* webbing, three stopped, one left the webbing, and one continued moving for the duration of the trial. The greater variability of the distance travelled by the control group resulted in a greater sample variance, which is responsible for the marginal significance value. Examination with a dissecting microscope revealed that on *Avicularia* silk the setae of the larval flies which stopped had become entangled in the loose silk strands. The phorid larvae on the *Theraphosa* shedding mats were likewise observed under magnification and seen writhing around, coated with *Theraphosa* hair, having anchored themselves with their posterior appendages.

DISCUSSION

The tarantulas of the New World have evolved a unique defensive strategy utilizing urticating setae, which is a characteristic shared only with the Lepidoptera. The variety of hair types and apparent uses indicates the utility of such an adaptation. Why it is only found in the New World theraphosid fauna, however, remains a mystery.

No egg sac predators of *Theraphosa* have ever been recorded. As this is a little-studied species, this does not preclude their existence. It is obvious that both *Theraphosa* and *Megaphobema* are making an investment in both time and energy, as well as in paying the possible costs that shedding a complete coating of hairs may confer (i.e., loss of boundary layer effects, parasite defense).

Until we know more about the predators and parasites of *Theraphosa* there may be no way to know what selective forces induced the evolution of the unique behaviors leading to the inclusion of setae in egg sacs. However, evidence from experimental studies reported here allows some speculation about possible selective agents.

The vertebrate tests indicate that the silk-hair matrix has no negative effect on three mammalian species (although these species have no previous ecological or evolutionary exposure to theraphosid spiders). In its egg sacs *Theraphosa* uses a field of hairs that contains the lowest proportion of urticating hairs, and a hair type that is distinct from those used in individual defense against vertebrates. These findings argue against a hypothesis that this defensive mechanism is adapted to deter vertebrate predators. Additionally, during incubation, both *Theraphosa* and *Megaphobema* guard their egg sacs constantly and with vigor. This behavioral investment may be considerable, as *Theraphosa* in captivity attend the egg sac for 11 weeks until hatching (Marshall pers. obs.). As female *Theraphosa* will engage in typical defensive displays while holding the egg sac in their fangs, it seems likely that an attack by a large, vertebrate egg sac predator would be warded off at an early stage in the predatory sequence, or the female herself would be the target of attack. The tests with *Megaselia scalaris* larvae indicate that egg sac material with or without setae may be an effective barrier to penetration by larval parasitoids or scavengers. However, the behavior of *M. scalaris* larvae on the *Theraphosa* shedding mats indicates that the incorporated hairs function as a means of deterring parasites. During the molting process a spider is clearly more vulnerable to boarding (or re-boarding) by ectoparasites. On at least one occasion, a captive *Theraphosa* was seen to have a later instar

Megaselia sp. larvae moving about on one of its patellae as the spider prepared to molt. It is also noteworthy that while both *Theraphosa* and *Megaphobema* include setae in the egg sacs, only the species known to have the phorid ectoparasite spins a shedding mat which includes setae. This adds credence to the hypothesis that combining urticating hairs with silk is an adaptation against larval dipteran parasitoids.

ACKNOWLEDGMENTS

We wish to thank R. Raven and W. Robinson for identification of the spiders and flies, respectively; also the numerous people who have been of indispensable help in the field (in chronological order) A. Miles, G. Tavakilian, M. Modde, J. Lapp, Thomas, la famille Scolard, and S. Doumain. The senior author especially wishes to thank the Marshall family for their support and toleration of a *Theraphosa* colony in their basement during the early stages of his tarantula studies.

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CHROMOSOMES OF SIXTEEN SPECIES OF HARVESTMEN (ARACHNIDA, OPILIONES, CADDIDAE AND PHALANGIIDAE)

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ABSTRACT

Chromosomes of *Caddo agilis* (Caddidae) and fifteen species of Phalangidae were investigated. In three species, *Nelima satoi*, *N. similis*, and *Eumesosoma roeweri*, presence of XY-XX (male heterogametic) sex chromosome system was newly ascertained. On the other hand, ZW-ZZ (female heterogametic) sex chromosome system was suggested to be present in *Mitopus morio*. Effeminate ($2n = 20$) and normal ($2n = 18$) males of *Protolophus tuberculatus* were found to differ in chromosome number. A survey of known records of chromosome numbers in Caddidae and Phalangidae revealed a general trend that the number is greater in both Caddidae ($2n = 30$) and Phalangidae ($2n = 20-36$), fewer in Gagrellinae ($2n = 10-22$), and intermediate in Leiobuninae ($2n = 16-26$). Evolutionary trends are briefly discussed and compared with those in other arachnids.

INTRODUCTION

Studies on chromosomes of harvestmen are few with the counts of only 36 species being reported (Tsurusaki 1986). Chromosomal observation has, however, great importance in gaining comprehensive understanding of geographic variation, speciation process, and phylogeny of Opiliones, since chromosomes of harvestmen often vary among related species and sometimes among geographical populations within the same species (e.g., genus *Leiobunum*: Suzuki 1976a; Tsurusaki 1985a, b).

To advance our general knowledge of opilionid chromosomes, we have prepared chromosome slides over the past seven years. This paper is the result of this study and describes chromosomes of fifteen species of Phalangidae and one species of Caddidae.

MATERIALS AND METHODS

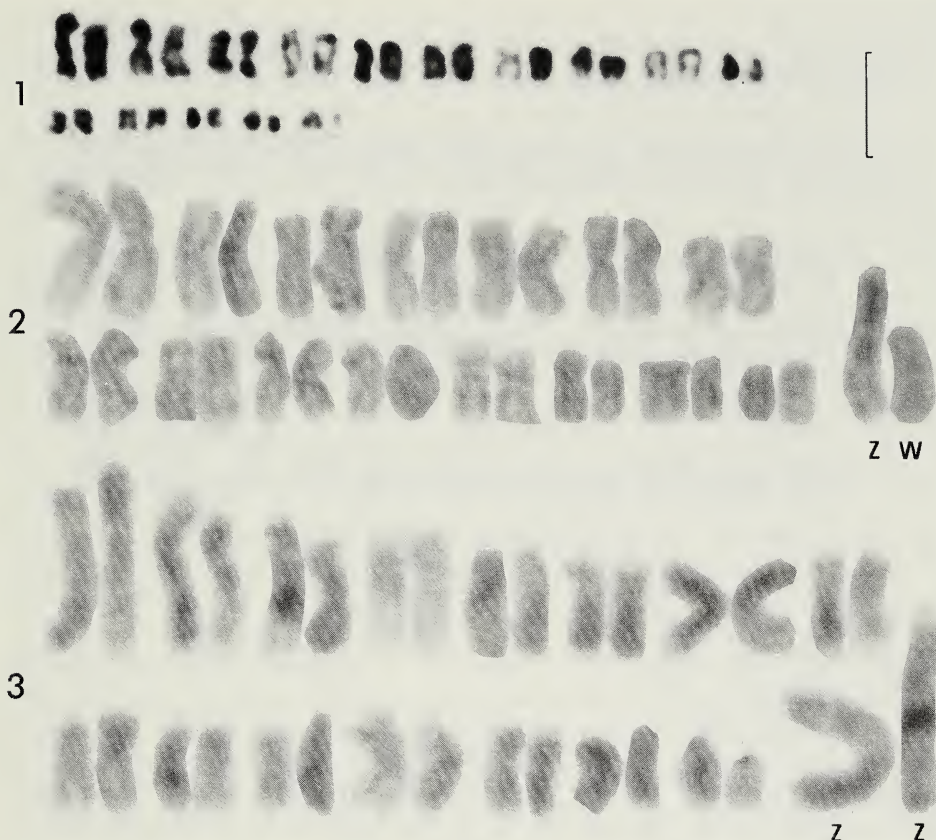
Sources of the specimens are listed in Table 1 and in the appendix. Chromosome preparations were prepared from testes or ovarian tissues of young adults and penultimates. Air-dried slides were made principally according to the method described in Tsurusaki (1985a) for the species from Japan and the

Table 1.—A list of materials used in the present study and obtained results. Detailed collecting data are given in the Appendix. M = male(s), F = female(s), juv. = juvenile(s). 2n chromosome number in parentheses denotes value inferred from haploid number alone. For distinction of the geographic forms of *Melanopa grandis*, see text.

Species	Locality	No. indiv. obs.	2n chrom. number		No. modal cell (M/F)
			M	F	
<i>Caddo agilis</i>	HOKKAIDO:Nopporo	9 juv. (F)	—	30	41
<i>Mitopus morio</i>	Is. Rishiri	3 juv.(2M, 1F)	32	32	9/3
<i>Homolophus arcticus</i>	HOKKAIDO: Wakasakanai	3 juv. (M)	24	—	25
<i>Homolophus rishiri</i>	Is. Rishiri	2 juv. (M)	24	—	13
<i>Phalangium opilio</i>	IDAHO:Moscow	1 M	32	—	1
<i>Dalquestia formosa</i>	TEXAS:Center Point	1 M	22	—	1
<i>Nelima satoi</i>	EHIME: Mt. Ishizuchi	2 juv. (F)	—	16	2
	FUKUOKA: Mt. Hiko	1 juv. (M)	16	—	11
<i>Nelima similis</i>	NAGANO:Takatô	4 M	20	—	11
<i>Leiobunum flavum</i>	TEXAS:L.Stubblefield	4 M	22	—	12
<i>Leiobunum townsendi</i>	TEXAS:Concho Co.	1 M	20	—	1
<i>Eumesosoma roeweri</i>	TEXAS:Concho Co.	2 M, 2F	22	22	3/2
	TEXAS:Kerrville	1 M	22	—	4
<i>Protolophus tuberculatus</i>	CALIFORNIA:San Anselmo	1M (1983)	(20)	—	5
	CALIFORNIA:San Anselmo	1 M (1984)	18	—	8
<i>Protolophus</i> sp.	CALIFORNIA:Little Sycamore Canyon	2 M	22	—	1
<i>Trachyrhinus rectipalpus</i>	TEXAS:Tilden	1 M	10	—	3
<i>Melanopa grandis</i>	Form 1 NAGANO:L.Misuzu	1 juv. (M)	20	—	5
	Form 1 NAGANO: Mt. Kirigamine	1 juv. (M)	20	—	5
	Form 2 TOTTORI: Mt. Daisen	3 M	20	—	6
	Form 3 FUKUOKA: Mt. Hiko	3 M	20	—	25
	Form 3 Is. Tsushima: Hidakatsu	1 M	20	—	16
	Form 1 Is. Tsushima: Mt. Ariake	1 M	20	—	8
<i>Paraumbogrella pumilio</i>	HOKKAIDO:Sunagawa	1 M	10	—	4

method in Cokendolpher and Brown (1985) for the species from the U.S.A. Of these methods, the procedures of the former were slightly modified in preparations after 1984 as follows: (1) use of Ringer's solution at the first step was abandoned and specimens were directly dissected in hypotonic solution. The tissues were removed and transferred to the same solution on another depression slide for hypotonic treatment; (2) as the hypotonic solution, 0.1% sodium citrate with colchicine (19 parts of 1% sodium citrate to one part of 0.1% colchicine solution) was used instead of pure 1% sodium citrate.

Metaphase chromosomes were serially arranged according to descending order of length (Figs. 1-3, 8-11, 18-24, 29-33). When a pair of heteromorphic chromosomes were observed only in either sex, those were considered as sex chromosomes. Haploid idiograms of each species were drawn based on a somatic metaphase plate with the clearest chromosome configurations by calculating percent ratios of length for each chromosome to the total length of the haploid chromosomes (TCL). TCL is the total of lengths of all haploid autosomes and one sex chromosome (X or Z) when detected. These idiograms should be considered as tentative since good metaphase spreads were scarce and results are based on only one or a few chromosomal spread(s). Nevertheless, they served to obtain rough compositions of karyotypes. Classification of chromosomal



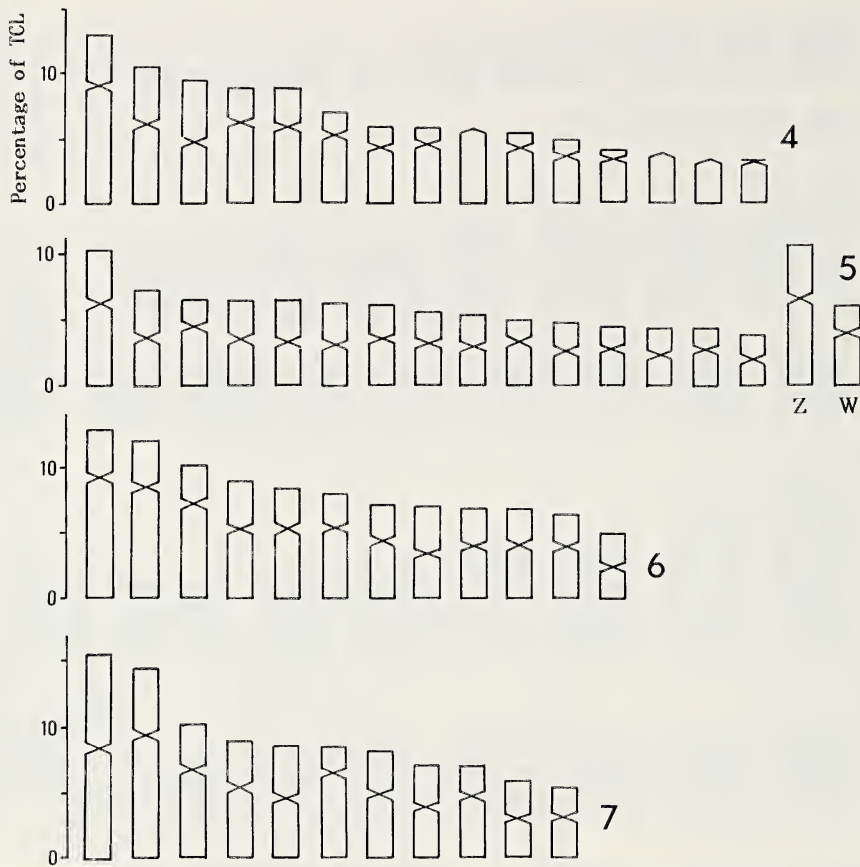
Figures 1-3.—Karyotypes of *Caddo agilis* and *Mitopus morio*: 1, *Caddo agilis*, female ($2n = 30$); 2, 3, *Mitopus morio* ($2n = 32$); 2, female; 3, male. Scale = 5 μm .

morphology was made according to Levans et al. (1964), where chromosomes are classified into the following five categories: metacentric ($1.0 \leq r < 1.67$), submetacentric ($1.67 \leq r < 3.0$), subtelocentric ($3.0 \leq r < 7.0$), acrocentric ($7.0 < r \leq \infty$) and telocentric, ($r = \infty$). $r = L/S$, where L and S are lengths of long arm and short arm, respectively.

RESULTS

Family Caddidae

***Caddo agilis* Banks.**— $2n$ (female) = 30 (Figs. 1, 4). Chromosomes were surveyed for females collected in 1982 from Nopporo, Hokkaido. A tentative idiogram based on some representative karyotypes (Fig. 1) is shown in Fig. 4. Chromosomes in which presence of short arm is unclear were prevalent in smaller ones; and chromosomes No. 9 or Nos. 13-15 were suggested to be telocentric or acrocentric. This species is considered to be parthenogenetic and only three males, one from North America and two from Japan, have been found (Gruber 1974; Suzuki and Tsurusaki 1983). The two males from Japan were collected in 1979 at Nopporo. However, no male has been found since then, so chromosomes of males of this species remain unknown.



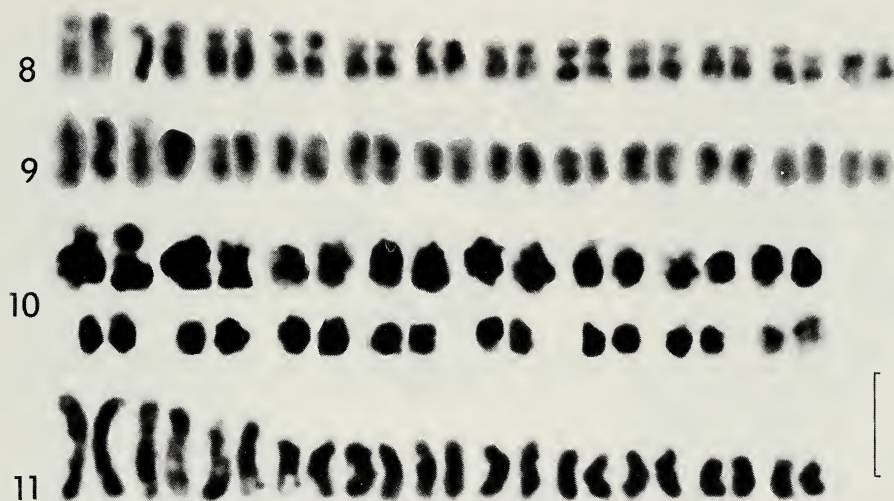
Figures 4-7.—Idiograms of *Caddo agilis* and three species of Phalangidae: 4, *Caddo agilis*, female; 5, *Mitopus morio*, female; 6, *Homolophus arcticus*, male; 7, *Dalquestia formosa*, male.

Family Phalangidae

Subfamily Phalangiinae

***Mitopus morio* Fabricius.**— $2n$ (male, female) = 32 (Figs. 2-3, 5). This conforms to the number reported by Sokolow (1930) based on specimens from westernmost area of European part of U.S.S.R. and by Jennings (1982) on specimens from northern England. Only one cell from a female (Figs. 2, 5) provided a chromosomal spread acceptable for karyotype analysis. The karyotype seems to consist of 15 pairs of autosomes and one heteromorphic pair of chromosomes. Compared with a chromosome spread from the male (Fig. 3), chromosomes of this heteromorphic pair appeared to be sex chromosomes and correspond to Z and W chromosomes. Z chromosomes are the largest and metacentric, whereas W is metacentric and similar in size to chromosome No. 7. Autosomes are metacentric except for Nos. 3 and 12 which are submetacentric.

***Homolophus arcticus* Banks.**— $2n$ (male) = 24 (Figs. 6, 8). No sex chromosomes were detected. The karyotype consisted of only metacentrics (Nos. 4, 5, 7-9, 12) and submetacentrics (others). In this respect, chromosome composition of this species is similar to that of *M. morio*.



Figures 8-11.—Karyotypes of males of four species of Phalangiidae: 8, *Homolophus arcticus* ($2n = 24$); 9, *Homolophus rishiri* ($2n = 24$); 10, *Phalangium opilio* ($2n = 32$); 11, *Dalquestia formosa* ($2n = 22$). Scale = 5 μ m.

***Homolophus rishiri* Tsurusaki.**— $2n$ (male) = 24 (Figs. 9, 12). This $2n$ number is the same as *H. arcticus*. Further analysis was not possible due to the indistinct chromosomal spread (Fig. 9). Numerous first meiotic metaphases showed 12 bivalents without exception (Fig. 12).

***Phalangium opilio* Linnaeus.**— $2n$ (male) = 32 (Fig. 10). Only one spermatogonial metaphase plate, which is not enough for detailed karyotype analysis, could be found; it showed $2n = 32$ clearly (Fig. 10). This number corresponds to that reported by Sokolow (1930) who studied the population in westernmost area of European U.S.S.R. However, this number does not agree with Juberthie (1956), who reported $2n = 24$ for specimens from Moulis, Ariège, France. Further survey is needed to confirm whether this incongruence in chromosome number means a different species.

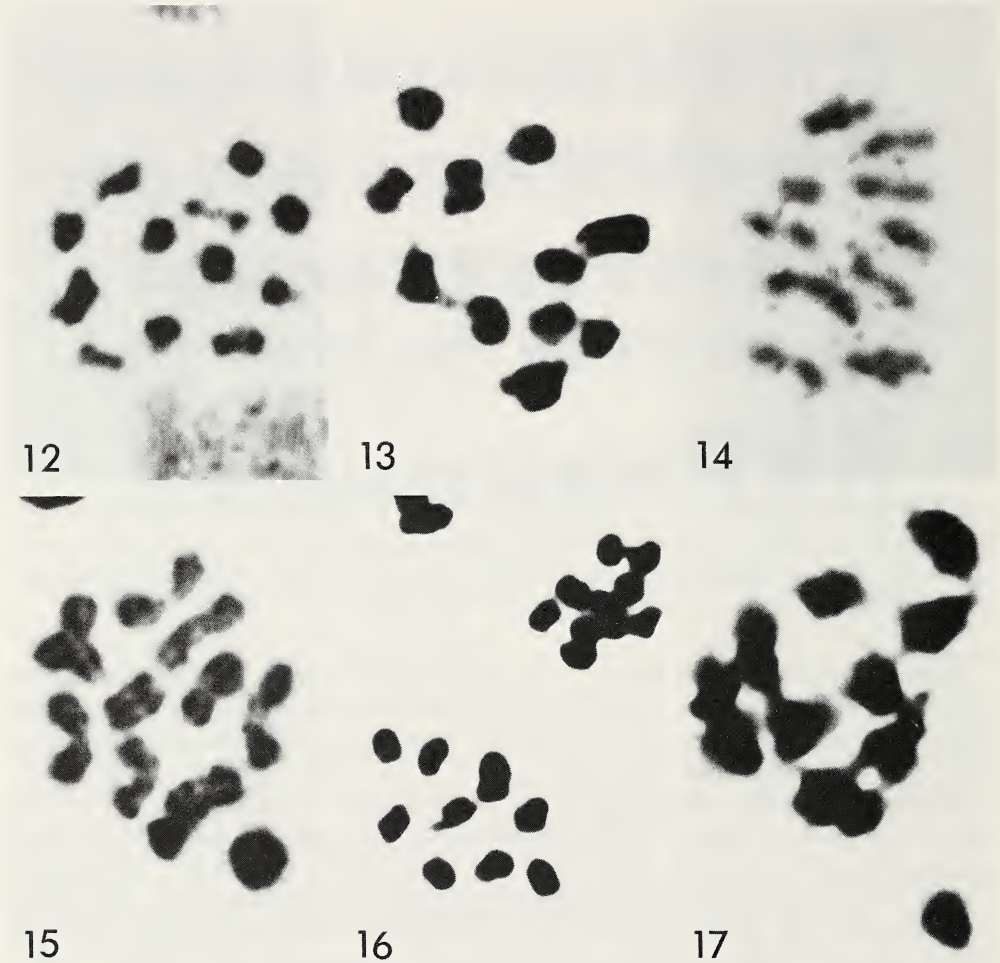
Subfamily unnamed

For comments on the placement of the genus *Dalquestia* Cokendolpher, see Cokendolpher (1984).

***Dalquestia formosa* (Banks).**— $2n$ (male) = 22 (Figs. 7, 11). No sex chromosomes were detected. Karyotype consists of four pairs of submetacentrics (Nos. 2, 3, 6, 9) and seven pairs of metacentrics (others).

Subfamily Leiobuninae

***Nelima satoi* Suzuki.**— $2n$ (male, female) = 16 (Figs. 18, 19, 25). The karyotype is composed of seven pairs of autosomes and one pair of male heterogametic sex chromosomes (male: XY, female: XX) (Figs. 18, 19). Autosomes are metacentric except for two pairs (Nos. 5, 7) being submetacentric



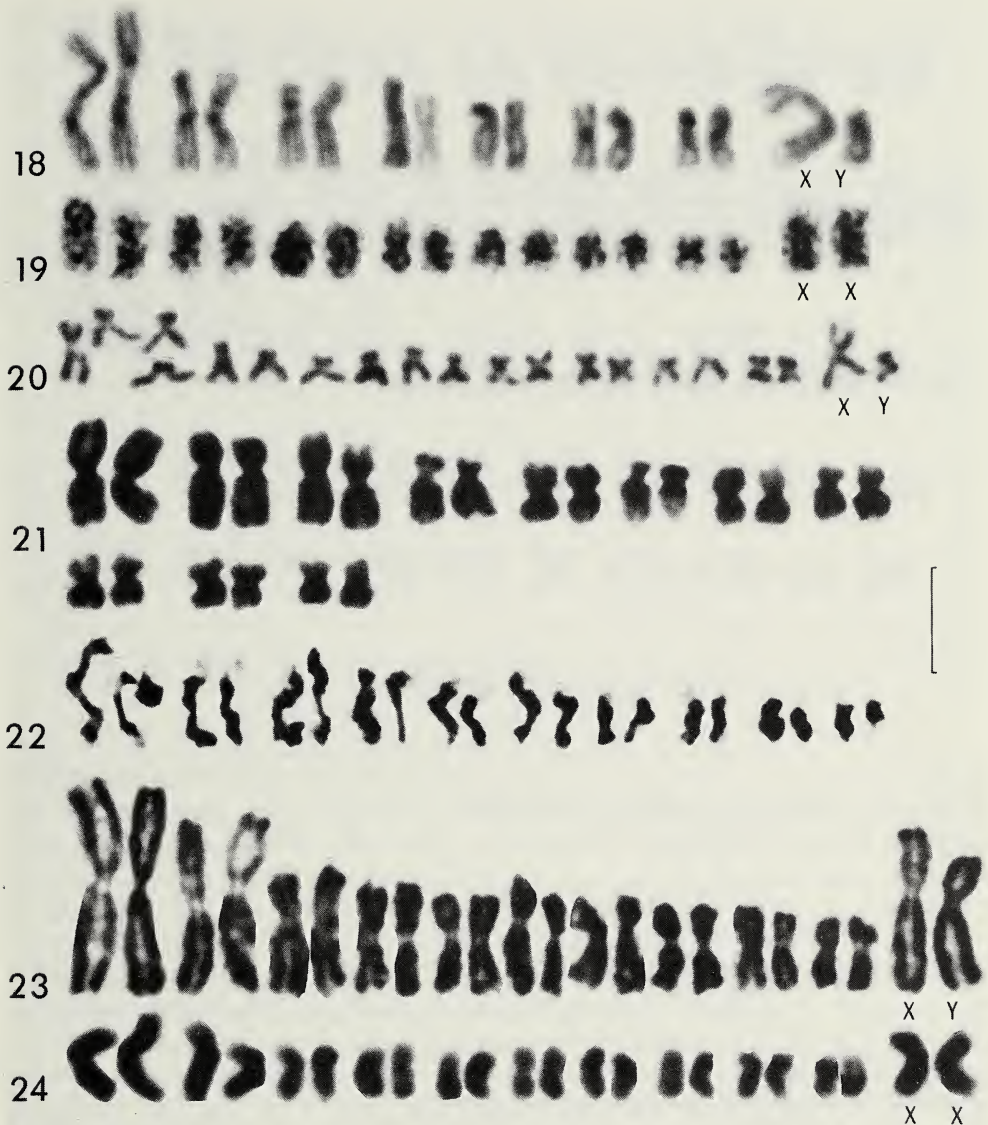
Figures 12-17.—Meiotic chromosomes in males: 12, *Homolophus rishiri*, metaphase I ($n = 12$); 13, *Dalquestia formosa*, metaphase I ($n = 11$); 14, *Melanopa grandis* (Mt. Ariake, Is. Tsushima), metaphase I ($n = 10$); 15, 16, *Protolophus tuberculatus*; 15, metaphase I ($n = 10$); 16, metaphase II ($n = 9$); 17, *Protolophus* sp., metaphase I ($n = 11$). Scale = 5 μ m.

(Fig. 25). The X chromosome is the second largest submetacentric, and Y is submetacentric similar in size to the shortest chromosome No. 7.

***Nelima similis* Suzuki.**— $2n$ (male) = 20 (Figs. 20, 26). The karyotype consisted of nine pairs of autosomes and one pair of heteromorphic sex chromosomes (Fig. 20). Autosomes are comprised of two pairs of submetacentrics (Nos. 2, 5) and seven pairs of metacentrics (others) (Fig. 26). The metacentric X and Y chromosomes are, respectively, the largest and the shortest.

***Leiobunum flavum* Banks.**— $2n$ (male) = 22 (Figs. 21, 27). The karyotype consisted of three pairs of submetacentrics (Nos. 4, 6, 8) and eight pairs of metacentrics (others). No sex chromosomes were discernible. This number, $2n = 22$, is the same as those reported in four species of *Leiobunum* C. L. Koch of North America (Parthasarathy and Goodnight 1958; Tsurusaki and Holmberg 1986).

***Leiobunum townsendi* Weed.**— $2n$ (male) = 20 (Fig. 22). Only one spermatogonial metaphase plate with 20 chromosomes was obtained (Fig. 22). Detailed karyotype is unknown.



Figures 18-24.—Karyotypes of five species of Leiobuninae: 18, 19, *Nelima satoi* ($2n = 16$); 18, male, Mt. Hiko; 19, female, Mt. Ishizuchi; 20, *Nelima similis* ($2n = 20$), male; 21, *Leiobunum flavum* ($2n = 22$), male; 22, *Leiobunum townsendi* ($2n = 20$), male; 23, 24, *Eumesosoma roeweri* ($2n = 22$); 23, male; 24, female. Scale = 5 μ m.

Eumesosoma roeweri (Goodnight and Goodnight).— $2n$ (male, female) = 22 (Figs. 23, 24, 28). The autosomes were composed of ten pairs of metacentrics (Fig. 28). The X chromosome is a metacentric similar in size to chromosome No. 2; while Y is a submetacentric and somewhat smaller than X.

Subfamily Sclerosomatinae (?)

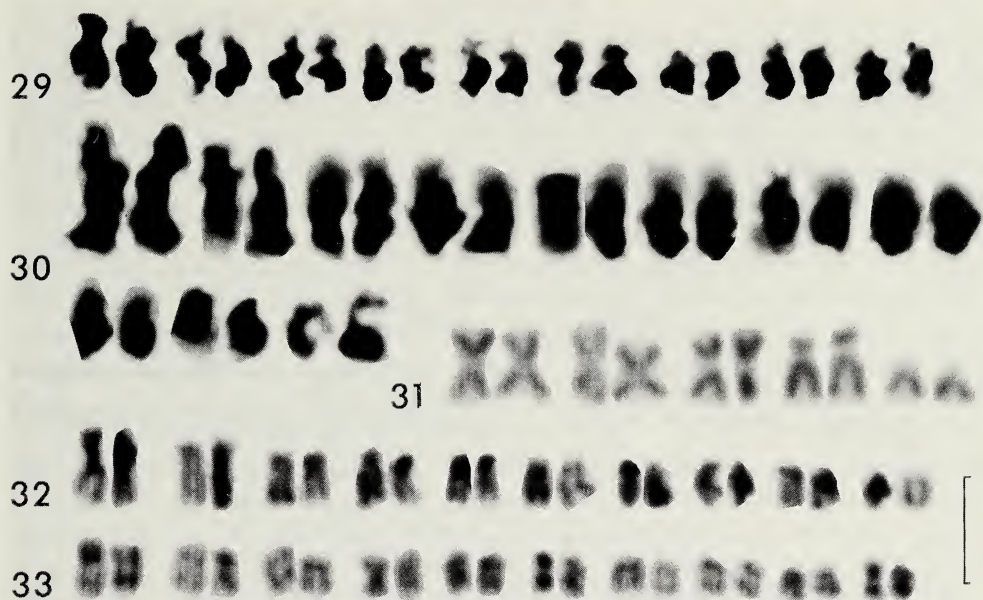
For the tentative placement of the genus *Protolophus* Banks, to which the following two species belong, in this subfamily, see Cokendolpher (1985). Large series of *Protolophus* spp. from various localities in the southwestern U.S.A.



Figures 25-28.—Idiograms of males of four species of Leiobuninae: 25, *Nelima satoi*; 26, *Nelima similis*; 27, *Leiobunum flavum*; 28, *Eumesosoma roeweri*.

reveal the presence in many populations of two types of males: a larger, more robust type and a smaller, effeminate type. This type of dimorphism is rare in harvestmen. The differences in the pedipalps are dramatic, with normal males often having femora twice as thick as those of effeminate males of the same population. One of us (J.C.C.) has thought for many years that these differences were due to a different number of molts for the two forms to reach adulthood. Attempts to rear *Protolophus* spp. in the laboratory (by J.C.C.) have failed, but successful copulations have been observed between single females and both types of males.

***Protolophus tuberculatus* Banks.**— $2n$ (male) = 18 and 20 (Figs. 15, 16, 29). Two males (one normal, one effeminate) collected from the same locality in San Anselmo, California but in different years, respectively 1983 and 1984, were used for chromosome observation. The result reveals the two forms have different chromosome numbers. That is, the effeminate male collected in the summer of



Figures 29-33.—Karyotypes of males of four species of Sclerosomatinae and Gagrellinae: 29, *Protolophus tuberculatus* ($2n = 18$); 30, *Protolophus* sp. ($2n = 22$); 31, *Trachyrhinus rectipalpus* ($2n = 10$); 32-33, *Melanopa grandis* ($2n = 20$); 32, Lake Misuzu; 33, Hidakatsu, Is. Tsushima. Scale = 5 μ m.

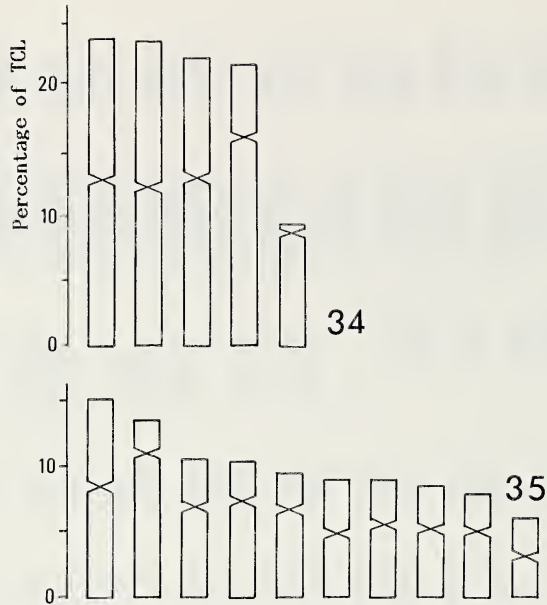
1983 showed $n = 10$ (hence it is expected to be $2n = 20$) in its first and second meiotic metaphase plates (Fig. 15), whereas the normal male from sampling in 1984 showed chromosome number $2n = 18$ and $n = 9$ (Figs. 29 and 16). Detailed karyotype of the latter is unknown, although most of the chromosomes seem to be submeta- or metacentric. Further study, including females, is needed to understand the implication of this discrepancy in chromosome number.

***Protolophus* sp.**— $2n$ (male) = 22 (Fig. 30). Only one spermatogonial metaphase spread with 22 chromosomes was obtained. Detailed composition of chromosomes is unknown, although most chromosomes seem to be metacentric or submetacentric (Fig. 30). Since this species could not be identified, we are depositing the specimen in the collection of the California Academy of Sciences, San Francisco.

Subfamily Gagrellinae

***Trachyrhinus rectipalpus* Cokendolpher.**— $2n$ (male) = 10 (Figs. 31, 34). The karyotype consists of three pairs of metacentric (Nos. 1-3), one pair of submetacentric (No. 4), and one pair of small acrocentric chromosomes (Figs. 31 and 34). No sex chromosomes were detected. This chromosome number, $2n = 10$, is the lowest reported in Opiliones, ranking with *Systenocentrus japonicus* Hirst and *Paraumbogrella pumilio* (Karsch) (Tsurusaki 1982; also see below).

***Melanopa grandis* Roewer.**— $2n$ (male) = 20 (Figs. 32, 33, 35). Chromosomes were surveyed for specimens from six localities which represent three different geographic forms defined as follows in terms of structure of male palpi (P) and female genital operculum (GO) (cf. Suzuki 1972).



Figures 34-35.—Idiograms of males of two species of Gagrellinae: 34, *Trachyrhinus rectipalpus*; 35, *Melanopa grandis*.

Form I: male with normal but robust P and female with three (sometimes two) -sectioned GO [figs. 1(6-8) and 3IJK].

Form II: male with robust P having trigger-shaped tibiae; female with two-sectioned GO [figs. 1(9) and 3H].

Form III: male with normal and slender P; female with unsectioned GO [figs. 1(5) and 3E in Suzuki, 1972].

In spite of the prominent geographic variation in external morphology, numbers of chromosomes were determined to be $2n = 20$ ($n = 10$) without exception. Chromosomes of this species were generally so small in size ($2.2 \mu\text{m}$ on average) that few chromosome spreads could be analyzed in detail. Of these, representative karyotypes from Lake Misuzu, Nagano Pref. (Form I) and Hidakatsu on Is. Tsushima (Form III), and an idiogram based on the former are shown in Figs. 32, 33 and 35, respectively. The karyotype consisted of five pairs of metacentrics (Nos. 1, 6-8, 10), four pairs of submetacentrics (Nos. 3-5, 9), and one pair of subtelocentrics (No. 2). No sex chromosomes were detected.

Paraumbogrella pumilio (Karsch).— $2n$ (male) = 10. On the basis of specimens from Sapporo, Hokkaido, Tsurusaki (1982) reported chromosomes of this species as $2n$ (male, female) = 10 and XY (male) - XX (female) in its sex chromosome constitution under the name *P. huzitai* Suzuki (see Suzuki 1985, for the name change). This time, a male collected from Sunagawa, which is located about 70 km northeast of Sapporo, was chromosomally examined. Although no chromosome spreads sufficient for analysis could be obtained, chromosome number was clearly counted as $2n = 10$.

DISCUSSION

Table 2 is a compilation of the number of chromosomes and sex chromosome system so far recorded of various opilionid species, belonging to Caddidae and Phalangiidae. A comparison at subfamilial level reveals that chromosome numbers tend to be greater in Caddinae, Caddidae ($2n = 30$) or Phalangiinae ($2n = 20-36$), fewer in Gagrellinae ($2n = 10-22$), and intermediate in Leiobuninae ($2n = 16-26$).

However, chromosome number often fluctuates within the genus, sometimes even within a species (e.g., *Leiobunum montanum* Suzuki: Tsurusaki 1985b). This forms a contrast with the situation in most spiders where the chromosome numbers are relatively stable at the familial level (Hackman 1948; Suzuki 1954; Datta and Chatterjee 1983). Difference in population structure between both groups of animals may partly explain this disparity. That is, probability that newly emerged chromosomal variants are fixed in a population may be relatively high in opilionids due to their low vagility which promotes inbreeding and drift. On the other hand, in spiders, inbreeding and drift would be unlikely to occur, since ballooning would facilitate both dispersal of the sibs and gene flow among populations. Consequently, even if a chromosomal mutation did occur within a population of spiders, the prospect that this mutant would predominate existent chromosomes would be low. Thus, karyotype evolution in spiders is expected to be conservative. Such correlation between population structuring and evolutionary rate of karyotypic evolution is found in various animal groups and is also theoretically supported (White 1978; Bush 1981).

On the other hand, in spite of great diversity in number of chromosomes, both meta- and submetacentrics overwhelmingly predominate in the component chromosomes of Opiliones, compared to telo- or acrocentrics (Figs. 4-7, 25-28, 34, 35; cf. also Tsurusaki 1985b). This fact suggests that Robertsonian translocation is not a main cause for the change of chromosome number. Further, this also makes a contrast with the situation in spiders where chromosomes are usually structured as telo- or acrocentrics (Hackman 1948; Suzuki 1954; Kageyama et al. 1978; Kageyama and Seto 1979). Primary factors for the difference in chromosome structure between the two groups are still incompletely known.

Sex chromosome composition in Opiliones has been determined as usually XY-XX (male heterogametic) based on *Paraumbogrella pumilio* and some species of *Leiobunum* (Tsurusaki 1982, 1985a, b; Tsurusaki and Holmberg 1986). In addition to these species, *Nelima satoi*, *N. similis*, and *Eumesosoma roeweri* were also revealed to have the same system of sex chromosomes in the present study. On the other hand, presence of female heterogamety with ZW (female) - ZZ (male) was suggested in *Mitopus morio*. It deserves attention, since no species with female heterogamety has hitherto been recorded in arachnids (White 1973; Bull 1983: 17). There is a possibility that this sex chromosome system predominates in species of Phalangiinae, since (1) we failed to detect any heteromorphic sex chromosomes in males of the other species of Phalangiinae examined in this work and (2) female heterogamety is also suggested in *Oligolophus aspersus* (Karsch), one of the relatives of *M. morio* (N. T. unpubl.). Further survey using material of both sexes of various species is needed. Other

Table 2.—Number of chromosomes and sex determination in various species of opilionids belonging to families Caddidae and Phalangiidae. M = male, F = female. 2n chromosome number in parentheses denotes the one inferred from haploid number alone. References are abbreviated as follows: 1, Jennings (1982); 2, Juberthie (1956); 3, Parthasarathy and Goodnight (1958); 4, Sharma and Dutta (1959); 5, Sokolow (1930); 6-12, Suzuki (1941, 1957, 1966, 1976a, 1976b, 1980, 1986); 13, Tomohiro (1940); 14-16, Tsurusaki (1982, 1985a, 1985b); 17, Tsurusaki and Holmberg (1986); NT, Tsurusaki unpubl.; PS, Present study.

Species	Locality	Sex	2n chrom. number	Type of sex determ.	Refer.
Family Caddidae					
<i>Caddo agilis</i> Banks	Japan: Hokkaido, Nopporo	F	30	—	PS
Family Phalangiidae					
Subfamily Phalangiinae					
<i>Oligolophus aspersus</i> (Karsch)	Japan: various localities	M,F	20	ZW(?)	6, NT
<i>Oligolophus tridens</i> (C. L. Koch)	U.S.S.R.: Leningrad	M	32	—	5
<i>Mitopus morio</i> (Fabricius)	U.S.S.R.: Leningrad	M	32	—	5
	England: northern part	M	32	—	1
	Japan: Is. Rishiri	M,F	32	ZW	PS
<i>Mitopus ericaeus</i> Jennings	England: northern part	M	32	—	1
<i>Opilio parientinus</i> (De Geer)	U.S.S.R.: Leningrad	M	24	—	5
<i>Homolophus arcticus</i> Banks	Japan: Hokkaido	M	24	—	PS
<i>Homolophus rishiri</i> Tsurusaki	Japan: Is. Rishiri	M	24	—	PS
<i>Phalangium opilio</i> Linnaeus	U.S.S.R.: Leningrad	M	(32)	—	5
	France	M	24	—	2
	U.S.A.: Idaho, Moscow	M	32	—	PS
<i>Rilaena triangularis</i> (Herbst) (= <i>Platybunus triangularis</i> : in ref. 5)	U.S.S.R.: Leningrad	M	(36)	—	5
Subfamily unnamed					
<i>Dalquestia formosa</i> (Banks)	U.S.A.: Texas	M	22	—	PS
Subfamily Leiobuninae					
<i>Nelima satoi</i> Suzuki	Japan	M,F	16	XY	PS
<i>Nelima similis</i> Suzuki	Japan: Nagano Pref.	M	20	XY	PS
<i>Leiobunum japonense</i> <i>japonicum</i> (Suzuki)	Japan	M	16	—	10

<i>Leiobunum japonicum japonicum</i> Müller	Japan	M,F	20	XY	6,17
<i>Leiobunum paessleri</i> Roewer	Canada: British Columbia	M	22	XY	17
<i>Leiobunum crassipalpe</i> Banks	U.S.A.: details unknown	M	22	—	3
<i>Leiobunum nigripes</i> Weed	U.S.A.: details unknown	M	22	—	3
<i>Leiobunum ventricosum</i> Wood	U.S.A.: details unknown	M	22(?)	—	3
<i>Leiobunum flavum</i> Banks	U.S.A.: Texas	M	22	—	PS
<i>Leiobunum townsendi</i> Weed	U.S.A.: Texas	M	20	—	PS
<i>Leiobunum rupestre</i> (Herbst)	U.S.S.R.: Leningrad	M	22	—	5
<i>Leiobunum hikocola</i> Suzuki	Japan: Kyushu, Mt. Hiko	M	18	XY	15
<i>Leiobunum montanum</i> Suzuki	Japan: various localities	M,F	18-26	XY	9,16
<i>Leiobunum hiasai</i> Suzuki	Japan: Yamanashi Pref.	M	(24)	—	15
<i>Leiobunum sadoense</i> Tsurusaki	Japan: Is. Sado	M	(18)	—	15
<i>Leiobunum kohyai</i> Suzuki	Japan: Honshu	M	20	XY	9,15
<i>Leiobunum hiraiwai</i> (Sato and Suzuki)	Japan: various localities	M,F	18-22	XY	7,11,NT
<i>Leiobunum curvipalpe</i> Roewer	Japan: various localities	M,F	24	XY	7,NT
<i>Eumesosoma roeweri</i> (Goodnight and Goodnight)	U.S.A.: Texas	M,F	22	XY	PS
Subfamily Sclerosomatinae (?)					
<i>Protolophus tuberculatus</i> Banks	U.S.A.: California	M	18,(20)	—	PS
<i>Protolophus</i> sp.	U.S.A.: California	M	22	—	PS
Subfamily Gagrellinae					
<i>Trachyrhinus rectipalpus</i> Cokendolpher	U.S.A.: Texas	M	10	—	PS
<i>Gagrellopsis nodulifera</i> Sato and Suzuki	Japan: Hiroshima Pref.	M	16	—	13
<i>Gagrellula ferruginea</i> (Loman)	Japan: various localities	M,F	10-22	—	6,12,NT
<i>Melanopa grandis</i> Roewer	Japan: various localities	M	20	—	PS

<i>Melanopa unicolor</i> Roewer	India	M	18	—	4
<i>Systemocentrus japonicus</i> Hirst	Japan	M	(10)	—	8
<i>Paraumbogrella pumilio</i> (Karsch)	Japan; Hokkaido	M	10	XY	14, PS

than these, Parthasarathy and Goodnight (1958) suggested the presence of XO-XX (male heterogametic) system in opilionids based on their observation on *Vonones sayi* (Simon) (= *V. ornata*: in their paper) of family Cosmetidae (suborder Laniatores). This statement is somewhat dubious, however, since diploid number of chromosomes of this species may not be 25 as they reported but far more numerous [probably $2n = 78$ (male, female): J.C.C. pers. obs.]. Nevertheless, the possibility that XO system also will be found in other opilionids cannot be excluded. The XO type and its derivatives (XXO, XXXO, etc.) are ordinary systems in ticks (Oliver 1981) and particularly in Araneae where these systems are exclusive (Hackman 1948; Suzuki 1954) except for four species of the salticid genus *Pellenes* Simon having $X_1X_2X_3Y$ male, $X_1X_1X_2X_2X_3X_3$ female system (Maddison 1982) and some populations of huntsman spider, *Delena cancerides* Walckenaer having a kind of multiple XY sex-determining mechanism (Rowell 1985).

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APPENDIX

Collecting data of the materials.—These are given by the following order: Locality, date collected (Unless the materials are dissected on the same day or day after, dates of fixation is also given in parentheses), collector (N. T. = N. Tsurusaki, J. C. C. = J. C. Cokendolpher), number of individuals (Number in parentheses denotes the number of specimens dissected. This number may be unequal to the one in Table 1, since there were several slides that contained no countable chromosomal spreads).

1. *Caddo agilis*. JAPAN: HOKKAIDO; Ebetsu; Nopporo, 18 June 1982 (N. T.), 6 females; same locality, 21 June 1982 (N. T.), 3 females.
2. *Mitopus morio*. JAPAN: HOKKAIDO; Is. Rishiri; Mt. Rishiri, From Oshidomari to Pon-yama, 30-320 m alt., 8 July 1984 (N. T.), 1 male, 5 juveniles (5 juveniles).
3. *Homolophus arcticus*. JAPAN: HOKKAIDO; Teshio-gun; Toyotomi-chô; Wakasakanai, 9 August 1985 (N. T.), 3 males, 1 female, 16 juveniles (10 juveniles).
4. *Homolophus rishiri*. JAPAN: HOKKAIDO; Is. Rishiri; Mt. Rishiri; Oshidomari route, 670-1000 m alt., 8 August 1985 (N. T.), 2 males, 1 female, 3 juveniles (3 juveniles).
5. *Phalangium opilio*. U.S.A.: IDAHO; Latan Co.; Moscow, 14 September 1983 (F. W. Merickel), 1 male.
6. *Dalquestia formosa*. U.S.A.: TEXAS; Kerr Co.; 3.2 km SSE Center Point. 16 September 1983 (W. Rogers), 1 male.
7. *Nelima satoi*. JAPAN: EHIME PREF.; Mt. Ishizuchi, From Tsuchigoya to Mt. Iwaguro, 1490-1745 m alt., 5 August 1982 (N. T.), 2 juveniles.
8. *Nelima similis*. JAPAN: NAGANO PREF.; Kami-Ina-gun; Takatô, Hokomochi Shrine, 780 m alt., 20 August 1982 (N. T.), 16 males, 7 females, 6 juveniles (4 males).
9. *Leiobunum flavum*. U.S.A.: TEXAS; Walker Co.; Sam Houston National Forest, Lake Stubblefield, 29 August 1984 (S. W. Taber), 6 males.
10. *Leiobunum townsendi*. U.S.A.: TEXAS; Concho Co.; Colorado River crossing at Highway 2134 (31°34'N - 99°41'W), 11 June 1983 (fixed 5 August 1983) (F. L. Rose, L. Robbins and K. W. Selcer), 1 male.
11. *Eumesosoma roeweri*. TEXAS: Concho Co.; Colorado River crossing at Highway 2134 (31°34'N - 99°41'W), 11 June 1983 (F. L. Rose, L. Robbins and K. W. Selcer), 2 males, 2 females; Kerr Co.; 6.4 km E of Kerrville, 17 May 1984 (S. R. Jones), 3 males, 1 female.
12. *Protolophus tuberculatus*. U.S.A.: CALIFORNIA; Marin Co.; San Rafael Ridge at 800 Fawn Drive, San Anselmo, 15 May 1983 (fixed 22 May 1983) (L. G. Frehofer), 1 male; same locality, 19 March 1984 (fixed 4 April 1984) (L. G. Frehofer), 1 male.
13. *Protolophus* sp. U.S.A.: CALIFORNIA; Ventura Co.; Little Sycamore Canyon, ca. 1.6 km N Pacific Coast Highway (35°5'N - 118°57'W), 28 June 1985 (fixed 1 July 1985) (J. C. C.), 2 males.
14. *Trachyrhinus rectipalpus*. U.S.A.: TEXAS; McMullen Co.; 36.8 km S of Tilden, 20 May 1985 (fixed 24 May 1985) (S. W. Taber), 1 male.
15. *Melanopa grandis*. JAPAN: NAGANO PREF.; Matsumoto; Lake Misuzu, 980 m alt., 29 June 1984 (fixed 5 July 1984) (N. T.), 1 juvenile; Mt. Kirigamine, Kowashimizu campground, 1630 m alt., 8 July 1982 (N. T.), 2 juveniles (1 juvenile).
- TOTTORI PREF.; Mt. Daisen, 760-1100 m alt., 9 August 1982 (N. T.), 14 males, 9 females (2 males).
- FUKUOKA PREF.; Mt. Hiko, 640-800 m alt., 31 July 1982 (N.T.), 7 males, 6 females (3 males).
- NAGASAKI PREF.; Is. Tsushima; Kamitsusima-chô, Hidakatsu, 50-60 m alt., 26 July 1982 (N. T.), 17 males, 18 females (3 males); Is. Tsushima; Izuhara, Mt. Ariake, 200-530 m alt., 27 July 1982 (N. T.), 9 males, 5 females (3 males).
16. *Paraumbogrella pumilio*. JAPAN: HOKKAIDO; Sunagawa, on a levee of River Penke-Utashinai, near the city hall, ca. 25 m alt., 24 September 1986 (N. T.), 1 female; same locality, 1 October 1986 (N. T.), 1 male, 1 female.

GROUND SURFACE ARACHNIDS IN SANDHILL COMMUNITIES OF FLORIDA

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ABSTRACT

Ground surface populations of scorpions, uropygids, pseudoscorpions, solifugids, opiliones, mites, and ticks were studied for two years using pitfall traps and herp arrays set in twelve sandhill communities throughout Florida. Three species of pseudoscorpions, 1 species each of uropygids, solifugids, and scorpions, 5 species of opiliones, and 2 species of ticks were collected. A total of 474 mites were collected. Abundance of pseudoscorpions, uropygids, and acari were significantly correlated with the total mass of plant litter.

INTRODUCTION

Arachnids associated with the different plant communities of Florida are poorly known. Recently Corey and Taylor (1987, 1988, 1989) described the scorpion, pseudoscorpion, opilionid, and spider faunas in pond pine, sand pine scrub, and flatwoods communities. Pseudoscorpion and spider faunas from a northwest Florida salt marsh were described by Rey and McCoy (1983).

This paper describes and compares the scorpion, pseudoscorpion, uropygid, solpugid, opilionid, mite, and tick faunas in twelve sandhill communities throughout Florida (Laessle 1958; Myers 1985).

STUDY SITES

Twelve sandhill communities were investigated from November 1986 through December 1988. Each study site was sampled for four days during each season of the year. Seasons were as follows: winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November). Study sites were located throughout Florida (Fig. 1). Site locations (and abbreviations) were: San Felasco Hammock (SF), Alachua Co.; Morningside Nature Center (MS), Alachua Co.; Spruce Creek Preserve (SC), Volusia Co.; Orange City (OC), Volusia Co.; Bok Tower Gardens (BT), Polk Co.; O'leno State Park (OL), Columbia Co.; Suwannee River State Park (SR), Suwannee Co.; Wekiwa Springs State Park (WS), Orange Co.; Sandhill Boy Scout Reservation (BS), Hernando Co.; Janet Butterfield Brooks Preserve (JB),

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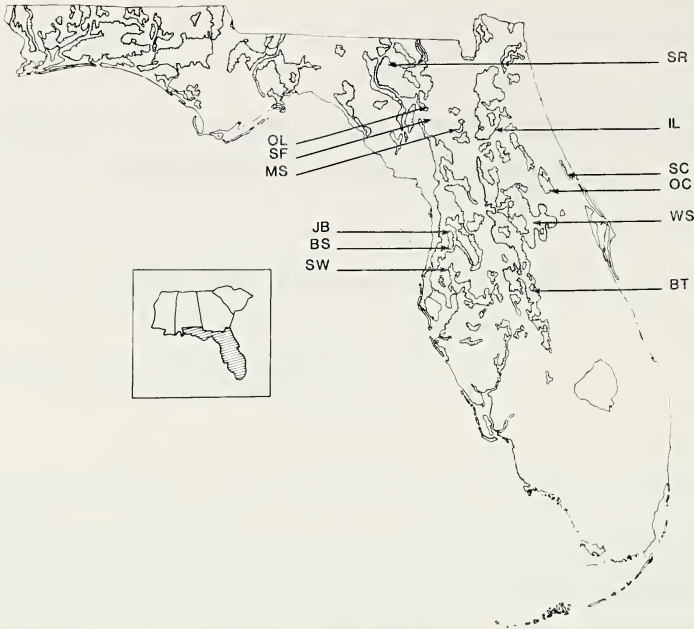


Figure 1.—Sandhill study site locations in Florida. See text for abbreviations. Sandhill distributions (stippled) are based on Davis (1980) and do not reflect minor sites of this community due to the scale of the illustration.

Hernando Co.; Interlachen (IL), Putnam Co.; Starkey Well Field Area (SW), Pasco Co.

Sandhills are xeric upland communities. Laessle (1958) and Myers (1985) provide a general summary of this community type. The tree layer is dominated by longleaf pine, *Pinus palustris*, and turkey oak, *Quercus laevis*. The understory consists chiefly of wiregrass, *Aristida stricta*, wild buckwheat, *Eriogonum tomentosum*, and saw palmetto, *Serenoa repens*.

METHODS

Arachnids were collected using 5 pitfall traps and 2 herp arrays. Pitfall traps were patterned after Muma (1973) and contained a 0.47 l mixture of ethylene glycol, water, and 95% ethanol in a ratio 2:1:1. The traps were randomly placed in each study site during the first collection period. During subsequent collections the traps were placed in the same location as in the first collecting period.

Two standard herp arrays of drift fences were also used to collect arachnids (Campbell and Christman 1982). Each array consisted of four sheet metal arms (7.6 m long) arranged to correspond to the cardinal directions. Two pitfall traps (21.14 l plastic buckets) were placed at the ends of each arm, and did not contain a preservative. Arachnids were removed from pitfalls daily. Two funnel traps made of fine-mesh wire screen were placed on each side of the sheet metal. The funnels were located at the midpoint of each arm.

Identification.—All specimens were identified to lowest possible taxon. James C. Cokendolpher, Texas Tech University, identified the opilionids. William B. Muchmore, University of Rochester, identified the pseudoscorpions. All other

Table 1.—Arachnid fauna collected in sandhill communities in Florida. See text for abbreviations.

ORDER Species	Collection sites												Totals
	SF	MS	SC	OC	BT	OL	SR	WS	BS	JB	IL	SW	
SCORPIONIDA													
<i>Centruroides hentzi</i> (Banks)	2	17	20	5	50	3		10	9	15	7	23	161
PSEUDOSCORPIONES													
<i>Planctolpium peninsulae</i>													
Muchmore			1	4	1	1			4	1	4		16
<i>Novohorus obscurus</i>													
(Banks)			1					1				1	3
<i>Paratemnus elongatus</i>													
(Banks)						1			1	1			3
UROPYGI													
<i>Mastigoproctus giganteus</i>													
(Lucas)			3	8									11
SOLPUGIDA													
<i>Ammotrechella stimpsoni</i>													
(Putnam)					4					1			5
OPILIONES													
<i>Leiobunum aurugineum</i>													
Crosby & Bishop		42	1	18		9	1		58	64	12	1	206
<i>L. bimaculatum</i> Banks	2			1		7	4		1				15
<i>Eumesosoma nigrum</i> (Say)	1					1							2
<i>Hadrobunus</i> sp.	7	36	9	13		6	12		25	8	6	2	124
<i>Vonones ornata</i> Say	1	3	1		1	1	2	5	1	8		1	24
ACARINA													
Mites	14	32	166	13	8	89	84	6	33	16	9	4	474
Ticks													
<i>Amblyomma americanum</i> (L.)			4			4							8
<i>Dermacentor variabilis</i> Say											2		2
TOTALS	23	130	206	62	64	122	103	22	132	114	40	32	1054

identifications were made by the senior author. Voucher specimens have been deposited at Florida State Collection of Arthropods, Division of Plant Industries, Gainesville, Florida.

Ground-level vegetation was sampled to determine if these microhabitat features were correlated with the abundance of arachnids. Twenty points were selected at random, and woody plants less than 2.54 cm in diameter at 1.37 m above the ground were counted in plots (3 x 2 m). Plot sides were used as line transects (5 m) to measure the canopy interception of grasses and herbs. Lastly, 10 plots (0.1 m² each) were randomly positioned and leaf litter collected, oven-dried, and the mass determined to the nearest gram. All measurements were taken during the second year of study. Pearson correlation coefficient was used to test the relationship between group abundance and ground level habitat features of the sandhill study sites (SAS Institute 1985).

RESULTS AND DISCUSSION

A total of 1054 arachnids belonging to 6 orders were collected. Species composition, total number of individuals trapped, and percentage collected with each method in the twelve study sites are listed in Tables 1 and 2. Comparison of seasonal and yearly abundance are in Table 3.

Table 2.—Percentage of arachnids collected by funnels (F), buckets (B), and pitfall traps (P).

ORDER Species	Methods		
	F	B	P
SCORPIONIDA			
<i>Centruroides hentzi</i> (Banks)	5.0	95.0	0.0
PSEUDOSCORPIONES			
<i>Planctolpium peninsulae</i> Muchmore	0.0	31.3	68.7
<i>Novohorus obscurus</i> (Banks)	0.0	100.0	0.0
<i>Paratemnus elongatus</i> (Banks)	0.0	33.3	66.7
UROPYGI			
<i>Mastigoproctus giganteus</i> (Lucas)	0.0	100.0	0.0
SOLPUGIDA			
<i>Ammotrechella stimpsoni</i> (Putnam)	0.0	75.0	25.0
OPILIONES			
<i>Leiobunum aurugineum</i> Crosby & Bishop	55.0	39.3	5.7
<i>L. bimaculatum</i> Banks	53.3	46.7	0.0
<i>Eumesosoma nigrum</i> (Say)	0.0	50.0	50.0
<i>Hadrobunus</i> sp.	19.4	39.3	5.7
<i>Vonones ornata</i> Say	8.3	25.0	66.7
ACARI			
Mites	0.4	12.0	87.6
Ticks			
<i>Amblyomma americanum</i> (L.)	0.0	0.0	100.0
<i>Dermacentor variabilis</i> Say	0.0	0.0	100.0
TOTALS			

One-hundred and sixty-one scorpions of a single species, *Centruroides hentzi* (Banks), were collected. Correlation (r) of scorpion abundance with ground-level habitat features is given in Table 4. No significant correlations were found, but scorpions were less abundant where shrubs were more common and plant litter accumulation was greater. *Centruroides hentzi* is commonly found under stones, logs, litter, and also under bark of dead standing trees (Muma 1967).

Males represented 67.7% of the total number of scorpions collected, while females represented 19.3% of the total population. Twenty-one juveniles were collected. All juveniles were collected in March, May, November, and February. Corey and Taylor (1987) collected 86% of their *C. hentzi* population from July through September, with all juveniles being collected in September. They found the greatest number of individuals in sand pine scrub, an upland xeric community with a well-developed shrub layer (Laessle 1958; Myers 1985).

Table 3.—Percentage of arachnids collected by season and year in the twelve sandhill study sites.

Order	1st Year					2nd Year				
	Fall	Winter	Spring	Summer	Total	Fall	Winter	Spring	Summer	Total
Scorpionida	9.9	3.7	13.7	7.5	34.8	19.3	5.6	24.2	16.1	65.2
Pseudoscorpiones	0.0	13.6	9.1	4.6	27.3	0.0	0.0	50.0	22.7	72.7
Uropygi	18.2	0.0	0.0	0.0	18.2	54.5	0.0	0.0	27.3	81.8
Solpugida	20.0	0.0	0.0	0.0	20.0	20.0	0.0	60.0	0.0	80.0
Opiliones	13.9	20.1	15.5	12.3	61.8	10.2	15.0	3.2	9.8	38.2
Acari										
mites	36.2	5.1	23.0	4.2	68.5	1.3	5.9	12.9	11.4	31.5
ticks	10.0	10.0	60.0	0.0	80.0	0.0	0.0	20.0	0.0	20.0

Table 4.—Correlation (r) of arachnid abundance with ground-level habitat features of sandhill study sites in Florida. *= r value significant at $P < 0.05$.

Order	Correlation of arachnid abundance with habitat features		
	Shrub density (no./m ²)	Grass-herb ground cover (cm)	Mass of plant litter (g)
Scorpionida	-0.516	0.237	-0.349
Pseudoscorpiones	-0.158	-0.216	0.601*
Uropygi	-0.056	-0.022	0.590*
Solpugida	-0.508	0.510	-0.330
Opiliones	-0.364	-0.209	0.094
Acari	-0.076	-0.354	0.620*

Two of the three species of pseudoscorpions found in sandhills, *Planctolpium peninsulae* Muchmore and *Novohorus obscurus* (Banks), were collected by Corey and Taylor (1987). They collected *P. peninsulae* from a sand pine scrub community and *N. obscurus* from pond pine, sand pine scrub, and pine flatwoods communities.

Pseudoscorpions spend most of their time in small crevices (Weygoldt 1969). Such microhabitat features on our study sites were associated with the bark of standing or fallen tree trunks and litter. Our sampling devices captured occasional individuals moving on the ground surface and probably underestimated the abundance of pseudoscorpions. A significant correlation ($r = 0.601$, $P < 0.05$) was found between pseudoscorpion abundance and mass of plant litter (Table 4).

Eleven Uropygi from a single species, *Mastigoproctus giganteus* (Lucas), were collected. These animals are often found under rotten logs and other debris on the surface of the ground (Muma 1967).

Five individuals of the solpugid *Ammotrechella stimpsoni* (Putnam) were collected. This is the only solpugid that occurs in peninsular Florida (Muma 1967).

A total of 371 opilions representing 5 species and 2 families were collected. *Vonones ornata* Say was the most common opilionid collected by Corey and Taylor (1987), and was found in sand pine scrub, pond pine, and pine flatwoods communities.

Opilions were not found to be correlated with ($P > 0.05$) shrub density, ground cover, or plant litter (Table 4).

Two individuals of *Eumesosoma nigrum* (Say) were collected. This species is found throughout the year in moist places under debris (Cokendolpher 1980).

Jennings, Houseweart, and Cokendolpher (1984) used pitfall traps to sample the epigeal phalangid fauna in strip clearcut and dense spruce-fir forest of Maine. They collected a total of 8 species, with 1 or 2 species being more abundant than the others in each habitat. Carter and Brown (1973) reported six species from pitfall traps in New Brunswick.

Tick and mites (Acari) represented 45.9% of the total arachnid population and were significantly correlated ($P < 0.05$) with the mass of plant litter (Table 4). Mites comprised 97.9% of the Acari. Two species of ticks were collected: *Amblyomma americanum* (Linnaeus) and *Dermacentor variabilis* Say.

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**A SAMPLING OF FOREST-FLOOR SPIDERS
(ARANEAE) BY EXPELLANT,
MOOSEHORN NATIONAL WILDLIFE REFUGE, MAINE**

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ABSTRACT

Spiders of 14 families, 34 genera, and at least 36 species were collected by formalin extraction from sub-litter habitats of the forest floor, Moosehorn National Wildlife Refuge, Washington County, Maine, in 1987. Species per family ranged from 1 to 7; the Erigonidae had the richest representation with 19.4% of all species. Most species (64.0%) were represented by sexually mature spiders; the ratio of female to male spiders was 3.2:1. Species of web-spinning spiders outnumbered species of hunting spiders 2 to 1. Numbers of spiders/0.25 m² circular plot ranged from 1 to 4; mean overall density of sub-litter spiders was 1.12 ± 0.17 SE, where $N = 36$ plots. Most (67.3%) of the spiders were associated with only one forest-stand type, possibly indicating species-habitat specificity.

INTRODUCTION

Spiders are increasingly recognized as important components of forest ecosystems (e.g., Moulder and Reichle 1972); however, relatively few studies have addressed the forest-floor araneofauna of particular forest-stand types. For northeastern forests of the United States and Canada, spruce-fir (*Picea-Abies*) stands have received the most attention (Freitag et al. 1969; Rudolf 1970; Carter and Brown 1973; Varty and Carter 1974; Jennings et al. 1988; Hilburn and Jennings 1988). Northern hardwood stands and mixed hardwood-softwood stands have received much less attention (Cutler et al. 1975), particularly those in Maine (Procter 1946). Most araneological studies of hardwood types concern forest-litter spiders of southern and midwestern deciduous forests (Bultman and Uetz 1984; Coyle 1981; Gasdorf and Goodnight 1963; Uetz 1979).

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As part of an investigation on the bioenergetics of the American woodcock, *Scolopax minor*, spiders were collected by a limited sampling technique from numerous forest-floor habitats of the Moosehorn National Wildlife Refuge in eastern Maine. Because detailed information was taken on tree-species composition and forest-stand type, these collections provide descriptive, habitat-associational information for the collected spider species.

METHODS

Spiders were collected from the soil surface following litter removal and formalin extraction on 36 circular 0.25-m² plots established temporarily at several locations on the Moosehorn National Wildlife Refuge, Calais and Baring Minor Civil Divisions, Washington County, Maine. The collections were made from 24 April to 16 June 1987, with plot-sampling dates distributed unevenly among months; April ($N = 3$ dates), May ($N = 14$), and June ($N = 6$). Plots were located at sites used by radio-marked woodcock and were sampled only once. Because of differential selection of forest stands by woodcock, the 36 sampling plots were distributed unevenly among forest-stand types, predominantly deciduous trees ($N = 27$ plots), coniferous trees ($N = 8$), and mixed coniferous-deciduous trees ($N = 1$). Forest-stand types were determined by a modified version (G. F. Sepik, Moosehorn NWR, unpubl.) of the Society of American Foresters (SAF) classification system (Eyre 1980). Each stand type was characterized by one or two predominant tree species. Deciduous tree species were: speckled alder, *Alnus rugosa*; bigtooth aspen, *Populus grandidentata*; quaking aspen, *P. tremuloides*; red maple, *Acer rubrum*; gray birch, *Betula populifolia*; and paper birch, *B. papyrifera*. Coniferous tree species were: balsam fir, *Abies balsamea*; spruces, *Picea* spp.; and eastern white pine, *Pinus strobus*. Common and species names of trees follow Little (1979).

At each site, a 0.25-m² ring (PVC pipe) was placed on the ground and all leaf litter removed down to the humus-mineral soil layer (Fig. 1). Spiders were not collected from the loose leaf litter; however, some litter-inhabiting species probably descended to the soil as the litter was removed. After litter removal, a 0.2% formalin solution was poured over the soil to extract spiders and earthworms (Reynolds et al. 1977). All spiders captured within 10 minutes following application of the expellant were placed in 75-80% ethanol.

For the most part, only sexually mature spiders were identified to species. Juvenile and penultimate stages were identified to family or generic level. Representative specimens of most spider species found will be deposited in the arachnid collections of the U.S. National Museum of Natural History, Washington, DC.

RESULTS

Spiders of 14 families, 34 genera, and at least 36 species were collected by formalin extraction from sub-litter habitats of the forest floor, Moosehorn National Wildlife Refuge, Maine, in 1987 (Table 1). Species per family ranged from 1 to 7. The Erigonidae had the richest representation with 19.4% of all species. Most (64.0%) of the species were represented by sexually mature spiders.

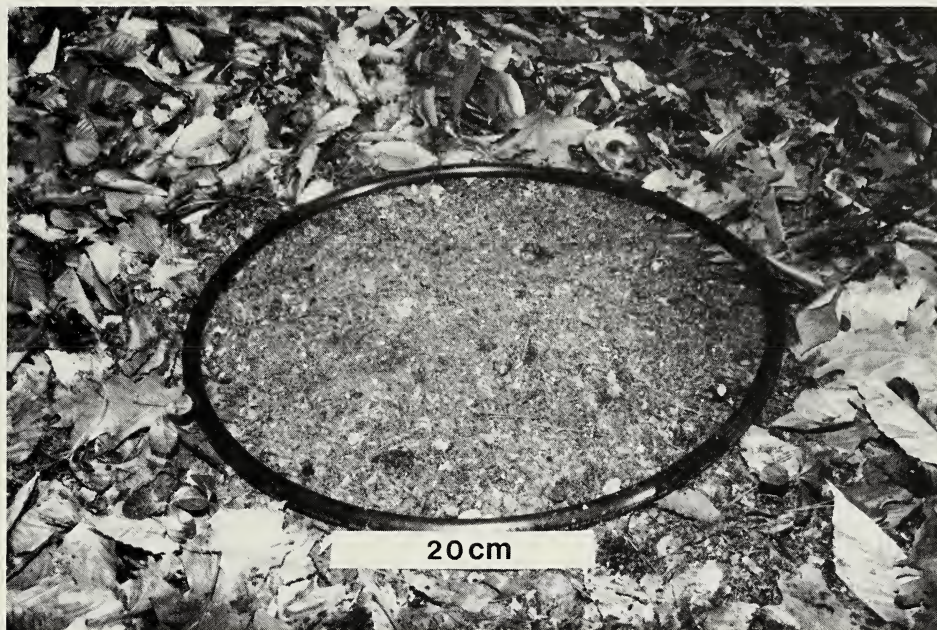


Figure 1.—Ring of PVC pipe used to delineate 0.25-m² plots. Spiders were collected from the sub-litter layer after removal of leaf-litter.

Species of web-spinning spiders (66.7%) outnumbered species of hunting spiders (33.3%) 2 to 1.

Eighty-one spiders were collected from the 36 circular 0.25-m² plots. Individuals were distributed unevenly among life stages; juveniles and penultimate stages comprised 58% of all specimens, while sexually mature males and females made up the remaining 42%. Overall, more females ($\Sigma = 26$) than males ($\Sigma = 8$) were collected.

Because of the limited sampling method used, the number of spiders per plot was very low, ranging from 1 to 4. The mean overall density of spiders collected from sub-litter habitats was 1.12 ± 0.17 SE, where $N = 36$ 0.25-m² circular plots.

The frequency distribution of forest-stand types among spider taxa ranged from 1 to 4 (Table 1). Most (67.3%) of the spiders were associated with only one forest-stand type; few (32.7%) were found in two or more stand types. As expected, spider species and individuals paralleled the apportionment of plots among forest-stand types (Table 2). Interestingly, nearly all (87.5%) of the hunting spiders were collected from stands with predominantly deciduous trees; few were collected from stands with coniferous trees.

DISCUSSION

Most of the species of spiders collected during this study are typical ground-inhabiting species often associated with forest leaf litter. Many have been taken by pitfall traps in spruce-fir forests of central and west-central Maine (Jennings et al. 1988; Hilburn and Jennings 1988); others have been collected from under stones and among dead leaves and by sifting spring-flood debris in Connecticut (Kaston 1981). The species we collected that appear unusual for forest-floor

Table 1.—Species and numbers of spiders collected from 36 circular 0.25-m² plots, sub-litter habitats of the forest floor, Moosehorn National Wildlife Refuge, Maine, 1987.

FAMILY	Number			Forest-stand type	
	Genus species	Males	Females		juv.
WEB SPINNERS					
AGELENIDAE		(0)	(3)	(5)	
<i>Agelenopsis</i> sp.				1	Alder
<i>Cicurina brevis</i> (Emerton)			3		Aspen-Maple; W. Pine-Aspen; W. Pine
<i>Cicurina</i> sp.				3	Aspen; Maple-P. Birch; Maple-G. Birch
<i>Wadotes</i> sp.				1	Maple
HAHNIIDAE		(0)	(1)	(1)	
<i>Antistea brunnea</i> (Emerton)			1		Alder-Aspen
Undet. sp.				1	W. Pine
AMAUROBIIDAE		(1)	(4)	(4)	
<i>Amaurobius borealis</i> Emerton		1	3		Alder; Aspen; Maple
<i>Amaurobius</i> sp.				1	Alder
<i>Callobius bennetti</i> (Blackwall)			1		Aspen-Maple
Undet. sp.				3	Alder; Alder-Aspen
DICTYNIDAE		(0)	(1)	(1)	
<i>Dictyna minuta</i> Emerton			1		Alder
<i>Dictyna</i> sp.				1	Balsam fir
THERIDIIDAE		(1)	(4)	(6)	
<i>Euryopsis argentea</i> Emerton		1			Spruce-Fir
<i>Robertus riparius</i> (Keyserling)			2		Alder; W. Pine
<i>Theridion aurantium</i> Emerton			1		Spruce-Fir
<i>Theridion sexpunctatum</i> Emerton			1		Balsam fir
<i>Theridion</i> sp.				3	Alder; Aspen
Undet. sp.				3	Alder; Maple; Balsam fir
LINYPHIIDAE		(0)	(2)	(2)	
<i>Lepthyphantes zebra</i> (Emerton)			2		Aspen; W. Pine-Aspen
<i>Prolinyphia marginata</i> (C. L. Koch)				1	Spruce-Fir
Undet. sp.				1	Aspen-Maple
ERIGONIDAE		(3)	(5)	(7)	
<i>Ceraticelus fissiceps</i> (O.P.-Cambridge)			1		Maple-G. Birch
<i>Diplocephalus cuneatus</i> Emerton			1		Aspen
<i>Hypselistes florens</i> (O.P.-Cambridge)		1			Aspen
<i>Maso sundevallii</i> (Westring)		1	1		Alder; Maple-G. Birch
<i>Tunagyna debilis</i> (Banks)			1		Aspen
<i>Walckenaëria auranticeps</i> (Emerton)		1			G. Birch
<i>Walckenaëria directa</i> (O.P.-Cambridge)		1			Maple-Aspen
Undet. sp.					Aspen; Maple-Aspen; W. Pine; Balsam fir
ARANEIDAE		(0)	(1)	(4)	
<i>Araneus</i> sp.				1	Spruce-Fir
<i>Mangora placida</i> (Hentz)			1		Balsam fir
<i>Mangora</i> sp.				1	Aspen
<i>Neoscona</i> sp.				2	Aspen; Maple-Aspen
TETRAGNATHIDAE		(0)	(0)	(1)	
<i>Tetragnatha</i> sp.				1	Aspen

	HUNTERS			
	(0)	(0)	(6)	
LYCOSIDAE				
<i>Pardosa</i> sp.			1	Aspen
<i>Pirata</i> sp.			3	Alder-Aspen; Maple-Aspen
<i>Trochosa</i> sp.			2	Aspen; W. Pine
GNAPHOSIDAE	(1)	(0)	(1)	
<i>Callilepis</i> sp.			1	Aspen-Maple
<i>Zelotes fratris</i> Chamberlin	1			Aspen-Maple
CLUBIONIDAE	(0)	(4)	(2)	
<i>Agroeca ornata</i> Banks		1		Aspen
<i>Clubiona</i> sp.			1	Aspen
<i>Phrurotimpus alarius</i> (Hentz)		3		Aspen; Aspen-Maple
<i>Phrurotimpus</i> sp.			1	Aspen
THOMISIDAE	(1)	(1)	(5)	
<i>Ozyptila</i> sp.			1	W. Pine
<i>Xysticus elegans</i> Keyserling	1	1		Aspen; Aspen-Maple
<i>Xysticus</i> sp.			4	Maple-Aspen; G. Birch; Maple-G. Birch; Balsam fir
SALTICIDAE	(1)	(0)	(2)	
<i>Habrocestum</i> sp.			1	Aspen
<i>Metaphidippus flaviceps</i> Kaston	1			Aspen
<i>Metaphidippus</i> sp.			1	Aspen

habitats include *Araneus* sp., *Mangora placida* (Hentz), *Neoscona* sp., *Hypselistes florens* (O.P.-Cambridge), *Prolinyphia marginata* (C. L. Koch), *Tetragnatha* sp., and *Metaphidippus flaviceps* Kaston. Because these species generally are associated with herb-shrub-tree strata, we suspect that individuals descended from upper levels to the forest floor.

Seven of the species of spiders collected by formalin extraction from forest-floor habitats of the Moosehorn National Wildlife Refuge have not been captured by extensive pitfall trapping in coniferous forests of Maine (Jennings et al. 1988; Hilburn and Jennings 1988). These include species represented by sexually mature spiders—*Dictyna minuta* Emerton, *Walckenaeria auranticeps* (Emerton), *Euryopis*

Table 2.—Distribution of forest-floor plots and collected spiders among three groups of forest-stand types, Moosehorn National Wildlife Refuge, 1987. *Groupings based on predominant trees; see text for tree species. †Mixed coniferous-deciduous trees. ††Conservative estimate; excludes undetermined species. Some species were found in more than one forest-stand type.

Parameter	N	Forest-stand type*					
		Deciduous		Coniferous		Mixed†	
		Σ	(%)	Σ	(%)	Σ	(%)
Plots	36	27	(75.0)	8	(22.2)	1	(2.8)
Species††							
web spinners	31	20	(64.5)	9	(29.0)	2	(6.4)
hunters	14	11	(78.6)	3	(21.4)	0	(0.0)
Individuals							
web spinners	57	40	(70.2)	15	(26.3)	2	(3.5)
hunters	24	21	(87.5)	3	(12.5)	0	(0.0)

argentea Emerton, and *Phrurotimpus alarius* (Hentz)—and species represented only by juveniles—*Callilepis* sp., *Habrocestum* sp., and *Ozyptila* sp. Little is known about their specific micro-habitat requirements; our data on forest-stand associations broaden the range of known habitats for these species.

No doubt, our sampling method (i.e., removal of litter without sorting for spiders) greatly contributed to the relatively low densities of spiders observed in sub-litter habitats of Maine. Hand sorting the litter, or extraction of leaf-litter spiders by Berlese or Tullgren funnel (Southwood 1978) should substantially add species and individuals to the list of spiders from forest-floor habitats.

Collection of spiders by expellant yielded a greater proportion (3.2:1) of females to males. Pitfall traps, on the other hand, are selectively biased toward capture of male spiders. Male spiders generally are more mobile and may move considerable distances in search of female spiders; hence, the sexes are seldom equally represented in pitfall-trap catches (Hallander 1967; Muma 1975).

Our study suggests that forest-floor spiders are not confined to the leaf-litter layer; we collected spiders from the sub-litter layer. After treatment with formalin, some spiders emerged from cracks and crevices in the soil. However, some of the spiders in our samples may have descended from upper layers, including leaf-litter and herb-shrub-tree strata.

Results of this study indicate that the araneofauna associated with forest-floor habitats of the Moosehorn National Wildlife Refuge is: (1) diverse, (2) composed of species and individuals that represent at least two spider-foraging strategies, and (3) possibly habitat specific, with few species shared in common among forest-stand types. Additional studies are needed to better define the araneofauna of any one forest-stand type. Studies also are needed to compare sampling methodologies (e.g., expellant vs pitfall-traps) at the same time, place, and stratum. On the basis of our study and previous studies (Bultman and Uetz 1984; Carter and Brown 1973; Uetz 1975, 1979), we predict that each forest-stand type will be composed of spider-species assemblages that are characteristic and descriptive for that type.

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**POPULATION DENSITIES OF SPIDERS (ARANEAE)
AND SPRUCE BUDWORMS (LEPIDOPTERA, TORTRICIDAE)
ON FOLIAGE OF BALSAM FIR AND RED SPRUCE
IN EAST-CENTRAL MAINE**

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ABSTRACT

Spiders of 10 families, 17 genera, and at least 22 species were collected from crown foliage samples of *Abies balsamea* (L.) Mill. and *Picea rubens* Sarg. in east-central Maine. Species of web spinners were more prevalent (68.2% of total species) among branch samples ($N = 613$ branches) than species of hunters (31.8%). Mean species per site ($N = 8$ sites) was 7.6 ± 1.2 . Numbers, life stages, and sex ratios of spiders differed between tree species; sex ratios were biased (G -test, $P \leq 0.001$) in favor of females. Spider densities per m^2 of foliage area generally were greater ($P \leq 0.05$) on red spruce ($\bar{X} = 12.0 \pm 1.3$) than on balsam fir ($\bar{X} = 7.2 \pm 0.9$), but sampling intensity was important. For intensely sampled sites, overall mean densities of spruce budworms/ m^2 of foliage were not significantly different ($P > 0.05$) between tree species. Spearman's rank correlation coefficients indicated that spider-budworm densities covaried weakly among study sites for each tree species; balsam fir ($\rho = 0.17$, $N = 343$), red spruce ($\rho = 0.15$, $N = 270$). Enhancement of spider populations through silvicultural treatments designed to favor spruces is proposed.

INTRODUCTION

The spruce budworm, *Choristoneura fumiferana* (Clem.), is the most widely distributed and destructive defoliator of spruce-fir (*Picea-Abies*) forests in North America (Talerico 1984). Conservation and enhancement of natural enemies of the spruce budworm are desirable goals of integrated pest management (IPM) systems directed against this forest pest (Simmons et al. 1984). Because spiders are predators of all life stages of the spruce budworm (Jennings and Crawford 1985), they are receiving increased attention from investigators (Renault and Miller 1972; Jennings and Collins 1987; Jennings and Houseweart 1989). Part of this interest stems from the potential to enhance or increase spider populations through habitat manipulations (Riechert and Lockley 1984; Provencher and Vickery 1988; Jennings et al. 1988; Riechert and Bishop 1990).

Spiders respond to structural features within habitats (Greenquist and Rovner 1976), and vegetation structure, complexity, and diversity are important parameters that influence spider numbers and richness (Lubin 1978; Greenstone 1984; Riechert and Gillespie 1986; Young 1989). Because of these attributes, it might be possible to enhance or increase spider populations in northeastern spruce-fir forests by selecting or favoring tree species that harbor abundant spiders. For example, Stratton et al. (1979) found that white spruce, *Picea glauca*, had more spiders (both numbers of individuals and numbers of species) than red pine, *Pinus resinosa*, or northern white-cedar, *Thuja occidentalis*, in Minnesota. Likewise, Jennings and Dimond (1988) found that spider densities generally were greater on spruces (white spruce and red spruce, *Picea rubens*) than on balsam fir, *Abies balsamea*, in Maine. By increasing the percentage tree-species composition of spruces in forest stands, it may be possible to increase population densities of arboreal spiders in these stands. However, we must first determine the species of spiders associated with northeastern conifers, assess their respective population densities, and determine their population enhancement potential.

In 1987, we collected additional data on the population densities of spiders and spruce budworms associated with tree-crown foliage of red spruce and balsam fir in east-central Maine. These data complement and support our earlier findings in east-central Maine (Jennings and Dimond 1988); they also provide historical records (1985-1987) of spider-budworm densities during the decline phase of a spruce budworm epidemic. In this paper we describe the arboreal spider fauna associated with balsam fir and red spruce, compare spider and spruce budworm population densities among study sites and between host-tree species, explore spider-budworm density relationships, and discuss possible pest management implications of our findings in east-central Maine.

METHODS

Study areas.—Eight forest stands in east-central Maine (Fig. 1) were sampled in 1987. Three of these stands were previously sampled in 1986 (Jennings and Dimond 1988). All sites were in open, spruce-fir stands that had declining populations of the spruce budworm. Study-site abbreviations and their locations by town, township, and county were:

- (MA)—Myra I, T32 MD, Hancock County
- (MY)—Myra II, T32 MD, Hancock County
- (DL)—Deer Lake, T34 MD, south, Hancock County
- (MR)—Machias River, T30 MD, Washington County
- (HM)—Hermon Mtn., T31 MD, Washington County
- (GP)—Georges Pond, Franklin, Hancock County
- (SH)—Sugar Hill, Eastbrook, Hancock County
- (NL)—Narraguagus Lake, T9 SD, Hancock County

At each location, trees along old logging roads and forest trails were selected for sampling based on tree dominance and accessibility. This resulted in variable-plot sizes with linear transects ranging from 0.5 to 1 km. At most sites, 10 dominant/codominant trees of each species (balsam fir, red spruce) were selected, flagged, and numbered for consecutive sampling on a weekly basis.

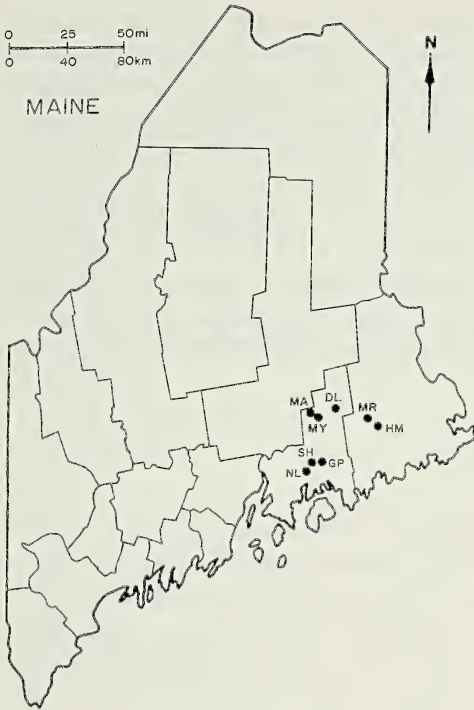


Figure 1.—Study-site locations in east-central Maine for sampling spider and spruce budworm densities, 1987. (See text for detailed descriptions of locations).

Branch samples.—We used a long, sectional pole pruner to cut one 45-cm branch from the upper crown half of each selected tree. The pole pruner was equipped with a cloth-basket attachment for catching any spiders and budworms dislodged when the branch was cut (Jennings and Collins 1987). Once lowered to the ground, severed branches and dislodged arthropods were removed from the basket and placed individually in labeled plastic bags for transport to the laboratory.

In the laboratory, technicians clipped the sample branches into small lengths (8-10 cm) and closely searched all foliage for spiders and spruce budworms. All collected spiders were stored in 2-dram vials containing 75% ethanol. Labels with study-site location, sample date, and branch-tree species were placed inside each vial.

For most study sites, selected trees were sampled at about weekly intervals beginning 27 May and ending 1 July 1987. However, balsam fir and red spruce were sampled only once (11 June 1987) at Georges Pond (GP), Narraguagus Lake (NL), and Sugar Hill (SH).

Spider identifications.—Sexually mature spiders were identified to species; juveniles, including penultimate stages, were identified to genus. However, juveniles of some philodromid spiders were identified to species (i.e., *Philodromus placidus* Banks) or species group (*aureolus*, *rufus*) based on color patterns of legs, carapace, and abdomen (Dondale and Redner 1978). Representative specimens of all identified species will be deposited in the arachnid collection, U. S. National Museum of Natural History, Washington, DC.

Data analyses.—Branch surface areas of balsam fir and red spruce were calculated by the formula: $A = (L \times W)/2$, where L is the foliated branch length and W is the maximum foliated width (Sanders 1980). Population densities of

both spiders and spruce budworms were expressed as numbers of individuals/m² of branch surface area. Because sampling intensities varied among study sites, we grouped the samples into high- and low-intensity sites. The Kruskal-Wallis Test (SAS Institute 1985) was used to compare spider-budworm densities among study sites and between tree species at $P = 0.05$. We used Spearman's rank correlation coefficient (ρ) to test for independence between spider and budworm densities. The G -statistic (Sokal and Rohlf 1981) was used to compare sex ratios of collected spiders, where the expected proportions were 0.50 males and 0.50 females. The G -statistic was also used to compare species composition of spiders by foraging strategy, where the expected proportions were: balsam fir—0.57 web spinners, 0.43 hunters; red spruce—0.64 web spinners, 0.36 hunters (Jennings and Dimond 1988).

RESULTS

Forest stands.—The study sites sampled in 1987 were similar to those previously investigated (Jennings and Dimond 1988). Balsam fir and red spruce were the principal softwood components, with occasional eastern white pine, *Pinus strobus*, eastern hemlock, *Tsuga canadensis*, and northern white-cedar. Hardwood components were maples (*Acer* spp.) and birches (*Betula* spp.). Most of the stands were open-grown with mean basal areas < 10 m²/ha. All stands were infested with the spruce budworm but their populations were declining.

Spider taxa.—Spiders of 10 families, 17 genera, and at least 22 species were collected from foliage of balsam fir and red spruce in east-central Maine (Table 1). Despite unequal sample sizes (balsam fir, $N = 343$ branches; red spruce, $N = 270$ branches), the species of spiders were distributed about equally between tree species, i.e., balsam fir, 19 species; red spruce, 20 species. However, web-spinning species were more prevalent among branch samples for both balsam fir (63.2%) and red spruce (70.0%). These observed species compositions did not differ significantly ($P > 0.05$) from the expected proportions (Jennings and Dimond 1988) for either tree species (balsam fir, $G = 0.28$; red spruce, $G = 0.32$).

The number of species per spider family ranged from one (Tetragnathidae) to five (Araneidae); the latter includes species identified only to generic-level (*Araneus* sp., *Neoscona* sp.).

Spider species composition varied among sites; $\bar{X} = 7.6 \pm 1.2$ SE, range 3 (SH) to 12 (DL, MR), where $N = 8$ sites. Only one species, *Grammonota angusta* Dondale, was common to all eight study sites sampled in 1987. *Dictyna brevitaris* Emerton, *Theridion* sp., *Philodromus* sp. (*rufus* grp.), and *Metaphidippus flaviceps* Kaston were each found on seven sites. Five species represented by adult spiders, *Ceraticelus atriceps* (O. P.-Cambridge), ERIGONIDAE undet. female, *Cyclosa conica* (Pallas), *Mangora placida* (Hentz), and *Eris militaris* (Hentz), were each found on only one study site.

Spider numbers, life stages, sex ratios.—Despite the unequal distribution of branch samples between tree species, over half (55.9%) of the total *sampled* spiders ($N = 315$) were from red spruce. Most of the *collected* spiders (13 lost, $N = 302$, Table 1) were females (47.4%), followed by juveniles (44.0%) and males (8.6%). Distributions of spider life stages for each tree species were: balsam fir—juveniles (41.5%), males (12.6%), females (45.9%); red spruce—juveniles (46.1%),

Table 1.—Spiders on foliage of *Abies balsamea* and *Picea rubens*, east-central Maine, 1987.

FAMILY <i>Species</i>	Balsam fir			Red spruce		
	Male	Female	juv.	Male	Female	juv.
WEB SPINNERS						
DICTYNIDAE						
<i>Dictyna brevitaris</i> Emerton	4	8		3	12	
<i>Dictyna phylax</i> Gertsch & Ivie		3			4	
<i>Dictyna</i> sp.			7			4
THERIDIIDAE						
<i>Theridion differens</i> Emerton	1				1	
<i>Theridion murarium</i> Emerton	1	2			1	
<i>Theridion</i> sp.			5			9
LINYPHIIDAE						
<i>Pityohyphantes costatus</i> (Hentz)		3			4	
<i>Pityohyphantes</i> sp.			1			1
ERIGONIDAE						
<i>Ceraticelus atriceps</i> (O. P.-Cambridge)					1	
<i>Grammonota angusta</i> Dondale	3	16		4	22	
<i>Grammonota pictilis</i> (O. P.-Cambridge)		1			1	
<i>Grammonota</i> sp.			1			
Undet. sp.					1	
ARANEIDAE						
<i>Araniella displicata</i> (Hentz)	1	2			3	
<i>Araniella</i> sp.			1			3
<i>Araneus</i> sp.			2			2
<i>Cyclosa conica</i> (Pallas)		1				
<i>Mangora placida</i> (Hentz)					1	
<i>Neoscona</i> sp.			1			1
TETRAGNATHIDAE						
<i>Tetragnatha</i> sp.			1			1
Subtotals	10	36	19	7	51	21
HUNTERS						
CLUBIONIDAE						
<i>Clubiona trivialis</i> C. L. Koch		3			4	
<i>Clubiona</i> sp.			5			3
PHILODROMIDAE						
<i>Philodromus exilis</i> Banks	1	2			7	
<i>Philodromus pernix</i> Blackwall	1	1				
<i>Philodromus placidus</i> Banks	1	3	7		3	8
<i>Philodromus</i> sp. (<i>aureolus</i> grp.)			5			4
<i>Philodromus</i> sp. (<i>rufus</i> grp.)			7			16
THOMISIDAE						
<i>Xysticus punctatus</i> Keyserling		1			2	
<i>Xysticus</i> sp.			1			6
SALTICIDAE						
<i>Eris militaris</i> (Hentz)		1				
<i>Eris</i> sp.						1
<i>Metaphidippus flaviceps</i> Kaston	4	15		2	14	
<i>Metaphidippus</i> sp.			12			18
Subtotals	7	26	37	2	30	56
TOTALS	17	62	56	9	81	77

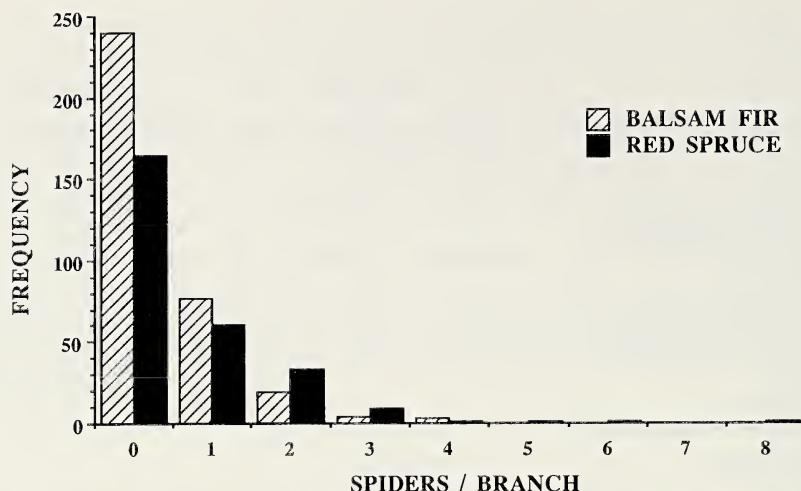


Figure 2.—Frequency distribution of spiders on balsam fir and red spruce branches, east-central Maine, 1987.

males (5.4%), females (48.5%). Sex ratios of males to females were: balsam fir, 1:3.6; red spruce, 1:9.0; both tree species, 1:5.5. All comparisons of spider sex ratios were highly biased ($P \leq 0.001$) in favor of females: balsam fir, $G = 27.2$; red spruce, $G = 66.2$; both tree species, $G = 89.2$.

The number of spiders per branch ranged from 0 to 4 for balsam fir; from 0 to 8 for red spruce (Fig. 2). Red spruce branches tended to have more spiders/branch than balsam fir. For example, 17.0% of the red spruce branches ($N = 270$) had 2 or more spiders/branch, whereas only 7.6% of the balsam fir branches ($N = 343$) had 2 or more spiders/branch.

Spider densities.—For both high- (> 10 branches/site) and low- (10 branches/site) intensity samplings of balsam fir, spider populations/ m^2 of foliage area varied among study sites (Table 2, column \bar{X} 's). However, spider populations/ m^2 of red spruce foliage did not differ significantly among study sites regardless of sampling intensity.

Spider densities generally were greater on red spruce than on balsam fir (Table 2, row \bar{X} 's); overall, these differences were significantly greater for the high-intensity sites sampled in 1987. Conversely, overall spider densities were not significantly different between tree species for the low-intensity sites.

Spider densities also varied by sampling date (Fig. 3). Mean densities on red spruce trees exceeded those on balsam fir trees 10 out of 14 sampling dates. For both tree species, mean densities generally declined as the season progressed.

Budworm densities.—Densities of spruce budworm larvae and pupae/ m^2 of foliage also varied among study sites for both tree species (Table 3, column \bar{X} 's). For high-intensity sites, overall mean densities were not significantly different between tree species (Table 3, row \bar{X} 's). However, for low-intensity sites, the overall mean density was significantly greater on balsam fir than on red spruce.

Spider-budworm density relationships.—Spider and spruce budworm densities covaried among study sites for each tree species; however, most of the correlations were weak ($(\rho) < 0.30$) and many were nonsignificant ($P > 0.05$), especially for low-intensity sites. Over all sites and sampling intensities, there was

Table 2.—Densities of spiders/m² of balsam fir and red spruce foliage, east-central Maine, 1987. Within each sampling group (high-low), column means (ab, a'b'), and row means (xy) followed by the same letter(s) are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$. * = MA classed as both high- and low-intensity site.

Spiders $\bar{X} (\pm SE) / m^2$ of foliage						
1987 Sites	No. branches sampled	Balsam fir		No. branches sampled	Red spruce	
HIGH-INTENSITY SITES						
HM	60	11.5 acx	(3.6)	59	10.3 ax	(2.2)
MR	59	9.8 ax	(1.6)	60	13.9 ax	(2.7)
MY	49	6.0 bcx	(1.6)	50	9.8 ax	(2.5)
DL	60	5.4 bcx	(1.6)	60	13.5 ay	(3.0)
MA*	85	4.4 b	(1.2)			
All	313	7.2 x	(0.9)	229	12.0 y	(1.3)
LOW-INTENSITY SITES						
GP	10	14.8 a'x	(4.4)	10	18.4 a'x	(5.5)
NL	10	13.3 a'b'x	(5.3)	10	9.2 a'x	(4.3)
SH	10	3.0 b'x	(2.2)	11	10.3 a'x	(4.2)
MA*				10	17.6 a'	(5.5)
All	30	10.4 x	(2.5)	41	13.8 x	(2.4)

little difference between tree species; balsam fir ((rho) = 0.17, $P = < 0.01$, $N = 343$), red spruce ((rho) = 0.15, $P = 0.01$, $N = 270$).

DISCUSSION

Spider taxa.—The species of spiders we collected from foliage of balsam fir and red spruce are typical arboreal spiders of northeastern spruce-fir forests. All of the identified species collected during this study previously have been taken from coniferous-tree foliage in east-central Maine (Jennings and Dimond 1988). Many of the same species also have been found on red spruce foliage in northern Maine (Jennings and Collins 1987). Based on their relative abundance, species common to arboreal habitats of Maine's spruce-fir forests include *Dictyna brevitorsus* Emerton, *Theridion murarium* Emerton, *Pityohyphantes costatus* (Hentz), *Grammonota angusta* Dondale, *Araniella displicata* (Hentz), *Clubiona trivialis* C. L. Koch, *Philodromus exilis* Banks, *P. placidus*, and *Metaphidippus flaviceps* Kaston. Five of these species—*D. brevitorsus*, *G. angusta*, *P. exilis*, *P. placidus*, and *M. flaviceps*—comprised 46.0% of all collected spiders in this study.

Apparently, none of the commonly collected species exhibited a definite habitat preference for either tree species; their relative abundances were about the same on balsam fir and on red spruce. The salticid, *M. flaviceps*, was slightly more abundant on balsam fir (Table 1), which is consistent with our earlier study (Jennings and Dimond 1988). We conclude that the erigonid, *G. angusta*, is much more prevalent on foliage of balsam fir and red spruce than its congeneric, *G. pictilis* (O. P.-Cambridge). Loughton et al. (1963) reported that *G. pictilis* was one of the most abundant spiders on balsam fir foliage at Fredericton, New Brunswick; however, according to Dondale (1959), most early collections and identifications of *Grammonota* in the Northeast refer to *G. angusta*, not *G. pictilis*.

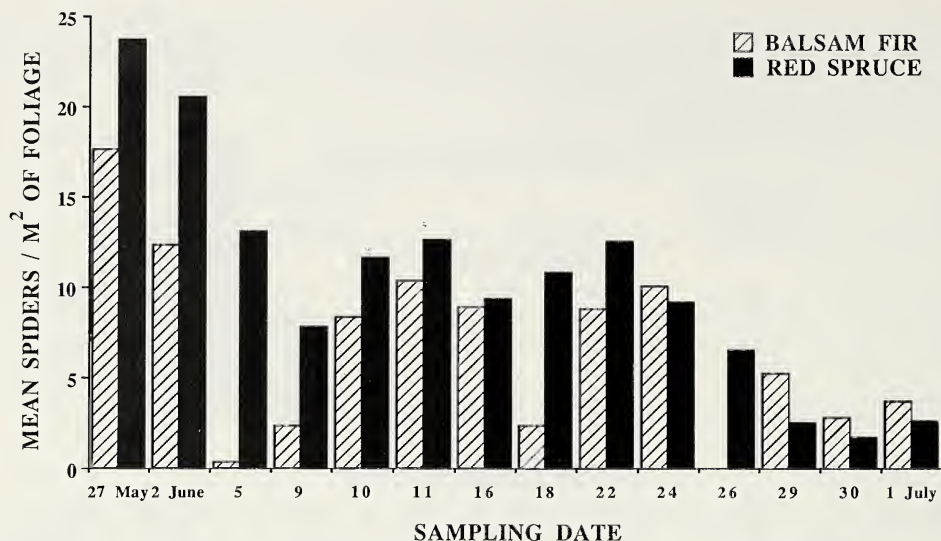


Figure 3.—Mean density of spiders/m² of foliage by sampling date, balsam fir and red spruce, east-central Maine, 1987.

Our observed differences in spider species composition by foraging strategy (web spinner, hunter) are consistent with earlier findings (Jennings and Dimond 1988; Loughton et al. 1963). The arboreal spider fauna of northeastern spruce-fir forests is dominated by the web-spinner guild, chiefly species of Erigonidae and Araneidae. The arboreal hunter guild in these forests consists mainly of species of Philodromidae, Thomisidae, and Salticidae.

Spider numbers, life stages, sex ratios.—Our results for these parameters complement and support earlier findings (Jennings and Dimond 1988), namely that: (1) more spiders are found on foliage of red spruce than on foliage of balsam fir; (2) for both tree species, spider individuals are distributed unevenly among life stages (juveniles, males, females); and (3) for both tree species, spider sex ratios (males:females) are biased in favor of females. No doubt, some of the observed differences in spider numbers, life stages, and sex ratios can be attributed to the reproductive cycles, developmental periods, and survivorships of individual species. For example, our sampling period spanned the time when both juveniles and adults of biennial species were present (e.g., *Philodromus placidus* and *Xysticus punctatus* Keyserling, see Dondale 1961, 1977). Because female spiders generally live longer than male spiders (Gertsch 1979), a biased sex ratio in favor of females can be expected. However, this does not fully explain the greater disparity in spider sex ratios on red spruce (1:9.0) as compared to balsam fir (1:3.6) that we observed in 1987. Because of the dense, closely compact foliage of red spruce, we suspect that resident female spiders gain some measure of protection from foliage-searching predators. If so, such females would have greater survival than their conspecifics on balsam fir, which has relatively open, flat foliage.

Spider-budworm densities.—The spider densities observed in 1987 generally are lower than those previously recorded (Jennings and Dimond 1988). For example, the mean overall density for balsam fir was 10.9 spiders/m² of foliage in 1985, and 8.5 spiders/m² in 1986 (Jennings and Dimond 1988); and 7.2 spiders/m² in

Table 3.—Densities of spruce budworms/m² of balsam fir and red spruce foliage, east-central Maine, 1987. Within each sampling group (high-low), column means (ab, a'b'), and row means (xy) followed by the same letter(s) are not significantly different, SAS Institute (1985), Kruskal-Wallis Test, $P = 0.05$. * = MA classed as both high- and low-intensity site.

Spruce budworms $\bar{X} (\pm SE)$ / m ² of foliage						
1987 Sites	No. branches sampled	Balsam fir		No. branches sampled	Red spruce	
HIGH-INTENSITY SITES						
HM	60	169.0 ax	(22.6)	59	79.0 by	(9.6)
DL	60	139.2 ax	(13.1)	60	123.2 ax	(13.2)
MR	59	46.4 bx	(9.3)	60	19.1 cy	(4.5)
MY	49	21.6 bx	(3.9)	50	13.3 cy	(4.2)
MA*	85	9.9 c	(2.4)			
All	313	73.9 x	(6.5)	229	60.5 x	(5.4)
LOW-INTENSITY SITES						
GP	10	340.1 a'x	(51.3)	10	237.9 a'x	(43.1)
NL	10	83.9 b'x'	(30.8)	10	26.9 b'x	(9.9)
SH	10	80.8 b'x'	(14.6)	11	69.0 bx	(24.7)
MA*				10	27.9 b'	(11.7)
All	30	168.2 x	(30.0)	41	89.9 y	(18.4)

1987 (Table 2). Similarly, for spruces (red and white), mean overall density was 16.3 spiders/m² in 1985 (Jennings and Dimond 1988); and, for red spruce, only 12.0 spiders/m² (high-intensity sites) and 13.8 spiders/m² (low-intensity sites) in 1987 (Table 2). Spruces were not sampled in 1986. We suspect that these declines in spider populations can be attributed to similar declines in potential prey populations (i.e., spruce budworms) in east-central Maine. Mean overall densities of spruce budworms generally were greater than 100/m² of foliage in 1985 and 1986 (Jennings and Dimond 1988); however, in 1987, similar densities usually were less than 100/m² of foliage (Table 3).

Despite individual site differences, our observations in 1987 further indicate that red spruce has more spiders than balsam fir. This conclusion is supported by the between-tree differences for overall site means (Table 2, red spruce, $\bar{X} = 12.0$ spiders/m²; balsam fir, $\bar{X} = 7.2$ spiders/m²; Kruskal-Wallis $\chi^2 = 7.7$, $P = 0.005$), and by the number of sampling dates (10 out of 14, Fig. 3) that mean spider densities on red spruce exceeded those on balsam fir. Nevertheless, sampling intensity affected these population-density estimates because between-tree differences were not detected for the low-intensity sites (Table 2, red spruce, $\bar{X} = 13.8$ spiders/m²; balsam fir, $\bar{X} = 10.4$ spiders/m²; Kruskal-Wallis $\chi^2 = 0.89$, $P = 0.35$). For future between-tree comparisons of spider densities, we recommend that trees be sampled over several dates and with sample sizes > 10 branches/tree species. Large sample sizes should help to stabilize variances within tree species and among study sites.

Spider-budworm relationships.—Our observations in 1987 further indicate that spiders may have been responding to available prey (budworm) populations in east-central Maine. This conclusion is supported by the fact that both spider and budworm populations generally declined together over the 3-year period, 1985-87, (this study; Jennings and Dimond 1988). Although the possible effects of density-independent factors (e.g., weather) on these populations cannot be ruled out, we

suspect that declines in budworm population densities concomitantly affected spider populations in a density-dependent fashion. However, more detailed studies are needed before we can fully understand spider-budworm interactions and their possible population density-relationships. Apparently, the weak correlations between spider-budworm densities/m² of foliage area observed during this study are to be expected; similar weak correlations were observed for spider-budworm densities on red spruce foliage in northern Maine (Jennings and Collins 1987).

Interestingly, individuals and species of all three spider families (Erigonidae, Theridiidae, Salticidae) previously identified as potentially important in spruce budworm dynamics (Loughton et al. 1963) were common among foliage samples taken from balsam fir and red spruce in east-central Maine. Future studies of spider-budworm interactions should concentrate on abundant species like *Grammonota angusta*, *Theridion murarium*, and *Metaphidippus flaviceps*. Because of their frequencies in coniferous-tree samples, relative abundances, and active foliage-searching behaviors, species of Thomisidae and Philodromidae also are likely predators of spruce budworm larvae. In laboratory feeding trials (Jennings, unpubl.), *Xysticus punctatus* readily accepted and fed on late instars (L₅ - L₆) of the spruce budworm. The predatory habits of this thomisid spider that frequents coniferous-tree foliage (Dondale and Redner 1978) warrant further investigation.

Spider-tree relationships.—Why does red spruce have more spiders/m² of foliage area than balsam fir? Stratton et al. (1979) attributed the greater spider diversity on white spruce foliage, as compared to that on foliage of red pine and northern white-cedar, to differences in plant physiognomy. We suspect that differences in foliage shape, structure, and density (number of needles per internode) also influence arboreal spider populations on red spruce and balsam fir. The availability of suitable habitat structures can limit spider population numbers (Riechert and Gillespie 1986); hence, the open, relatively flat needles of balsam fir probably provide less microhabitat space for web-spinning and foraging than the compact, curved needles of red spruce.

In Sweden, Gunnarsson (1988) found that percentage needle loss affected population densities of spiders on Norway spruce, *Picea abies* (L.). The density of large spiders (length ≥ 2.5 mm) was about twice as great in a stand with low needle loss as that in a stand with high needle loss. Because spiders are easier to detect on branches with few needles, Gunnarsson (1988) postulated that large spiders might be more vulnerable to bird predation.

Similarly, in the spruce-fir forests of Maine, defoliation by the spruce budworm could adversely affect resident spider populations on balsam fir, red spruce, and other host-tree species. Balsam fir is extremely sensitive to defoliation by the spruce budworm (Witter et al. 1984), and balsam fir usually receives more feeding damage and is more vulnerable to mortality than red spruce (Blum and MacLean 1984). Although we did not measure tree or branch defoliation during this study, balsam fir branches generally had fewer needles and more budworm feeding damage than red spruce. Such differences in foliage quantity may have contributed to the lower spider densities that we observed on balsam fir.

Pest management implications.—Results of this and our earlier study (Jennings and Dimond 1988) confirm that balsam fir generally has fewer spiders/m² of foliage area than red spruce. Balsam fir is the principal host of the spruce

budworm in eastern North America (Miller 1963); it is the tree species most severely damaged by the spruce budworm (Kucera and Orr 1981). The spruces—white, red, and black (*Picea mariana*)—on the other hand, are less vulnerable to damage by the spruce budworm (Blum and MacLean 1984). Forest entomologists have long attributed this relative “immunity” of spruces to host-insect asynchrony. The emergence of young budworm larvae from overwintering hibernacula in the spring may precede budbreak of spruces by several days; consequently, the larvae are forced to feed on old, less nutritious foliage (Morris et al. 1956; Greenbank 1963). Because balsam fir buds burst some 13 days before red or black spruce (Greenbank 1963), young instars of the spruce budworm are able to feed on new, nutritious foliage of balsam fir before similar foliage is available on spruces. These differences in host-foliage phenologies affect budworm survival and subsequent tree damage (Morris 1963; Greenbank 1963). However, based on our findings, we suggest that abundant spider populations also contribute to the apparent “immunity” of spruces to damage by the spruce budworm. If true, then management of forest stands to favor spruces over balsam fir may provide an indirect, cultural method to enhance these natural enemies of the spruce budworm.

But, can spider populations be enhanced or increased indirectly through silvicultural treatments designed to favor spruces over balsam fir? We believe that they can, because habitat-structural features are important determinants of spider populations (Riechert and Lockley 1984; Riechert and Gillespie 1986; Riechert and Bishop 1990). Silvicultural methods and guidelines are already available for increasing species composition and basal areas of spruces in northeastern spruce-fir forests (Frank 1979, 1985; Frank and Blum 1978). Such silvicultural treatments are advocated as a means to minimize forest-stand vulnerability to budworm damage (Blum and MacLean 1984). We predict that forest-stand treatments designed to favor spruces will also have a positive influence on resident spider populations through increases in favorable habitat structure. Our prediction needs to be tested by carefully designed and controlled experiments where both spider and potential prey densities are monitored before and after silvicultural treatments. Such information is needed before the onslaught of the next spruce budworm epidemic, which is expected in 25 or 35 years (Blais 1983; Royama 1984; Eidt 1989). Because of potential adverse impacts on prey diversity for spiders (Provencher and Vickery 1988), monocultures of red spruce, or any other conifer, should be avoided. Diversification of coniferous-tree habitats in northeastern spruce-fir forests is much more desirable and ecologically sound.

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**A NEW *GLENOGNATHA* (ARANEAE, TETRAGNATHIDAE)
FROM NEW JERSEY, WITH REDESCRIPTIONS OF
G. CENTRALIS AND *G. MINUTA***

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ABSTRACT

Both sexes of the tetragnathid spider *Glenognatha heleios* n. sp. are described and illustrated. Data about its natural history, ecology and phenology are included. A key to the *Glenognatha* species north of Mexico is presented. The types of two other *Glenognatha* species, *G. centralis* Chamberlin, 1925 and *G. minuta* Banks, 1898, from Panama and Baja California respectively, are redescrbed and illustrated.

INTRODUCTION

The spider genus *Glenognatha* Simon, 1887 includes 12 named species from North, Central and South America, and the Caribbean and Galapagos Islands, but there are also undescribed representatives in tropical America and the Pacific Islands (Levi 1980; Hormiga unpublished data). *Glenognatha* species north of Mexico were revised by Levi (1980). Here both sexes of *G. heleios* n. sp. are described and illustrated, and some data on the species' natural history are presented. The male of *G. centralis* Chamberlin, 1925 and *G. minuta* Banks, 1898 are redescrbed to provide adequate illustrations and descriptions because the original ones were not sufficient for identification purposes. It is not our purpose to assess or report the full range of the variation of *G. centralis* and *G. minuta* and therefore we did not study material other than the types. This paper is not meant to be a revision but it may serve as an addendum to Levi's revision (1980) of the *Glenognatha* north of Mexico.

According to the generic redescription given by Levi (1980), *Glenognatha* species have three teeth on the anterior margin of the chelicerae and four on the posterior. However we have examined specimens of an undescribed species from Venezuela that have five or six teeth on the anterior margin of the chelicerae and

six or seven on the posterior; these specimens also possess the pleural bars between coxae I-II and II-III, a character not common in *Glenognatha* (e.g., present in *G. mira* Bryant, 1945 between coxae II-III). These data suggest that the study of new species may add some changes to the diagnosis and description of *Glenognatha*.

METHODS

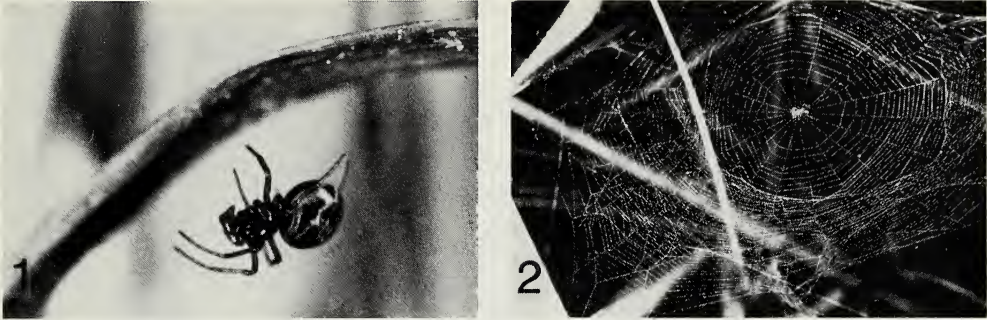
Specimens were examined and illustrated using a Wild M-5® stereoscopic microscope with a Wild 1.25X camera lucida; further details were studied using a Leitz Ortholux II® compound microscope. Female genitalia were cleaned by means of trypsin digestion after removal with sharpened needles. The male and female genitalia were mounted in Hoyer's medium on a microscope slide. Measurements are given in mm. Tarsal length of the male palp is given as the length of the cymbium. The left palp is illustrated, if not otherwise stated. Abbreviations used in the text are standard for Araneae.

The research on the ecology of *G. heleios* was conducted in an extensive intertidal marsh in the Mullica River—Great Bay estuarine system where Great Bay Boulevard crosses over Little Thorofare Creek near Tuckerton, Ocean County, New Jersey. *G. heleios* was sampled in habitats dominated by *Spartina alterniflora* Lois., the salt marsh cordgrass, which occurs in three distinct growth forms over an elevational gradient from 1.5 m below mean high water level to mean high water level (Redfield 1972). On the low marsh tall form *S. alterniflora* (50 to more than 200 cm tall) grows with reduced culm density along tidal creeks and bay edges (Adams 1963; Blum 1968). Further up the elevational gradient the tall form of *S. alterniflora* grades into stands of an intermediate growth form (30-50 cm tall) with an increased culm density (Niering and Warren 1980). On the high marsh near mean high water level, short form *S. alterniflora* (10-30 cm tall) grows at high densities. A more detailed description will be published elsewhere (Döbel et al. in prep.).

Two study plots (each 100 m² and separated by > 100 m) were established in each of the three *Spartina* habitats. On a bi-weekly basis from early May until late October, 1985 (11 dates in all), four samples were taken from each plot with a D-Vac® suction sampler (Dietrick 1961). Each sample consisted of four, 15 second random placements of a D-Vac® sampling head (0.0929 m²) on the vegetation surface. Arthropods were killed with ethyl acetate and transferred into jars containing 90% ethanol. Spiders were sorted to species and age class (adults and immatures) and counted.

Levi's key to the *Glenognatha* north of Mexico (Levi 1980) is modified as follows to include *G. heleios* (figures 255-289 and map 8 refer to his cited work):

1. Less than 3.0 mm total length; female with chelicerae not enlarged (fig. 272; Fig. 13); male with spur on chelicerae (figs. 276, 285; Figs. 5-8); embolus and conductor minute on huge spherical tegulum (figs. 278, 287; Figs. 9-11); southern Canada to Central America and West Indies (map 8)2
- Total length more than 3.5 mm; female with chelicerae enlarged (fig. 255); male without spur on chelicerae (fig. 266); embolus and conductor length greater than height of spherical tegulum (fig. 268); New Mexico, Arizona (map 8) *emertoni*



Figures 1, 2.—*Glenognatha heleios* n. sp.: 1, subadult male; 2, web (web diameter about 10 cm).

- 2. Paracymbium with a tooth in its anterior margin (Fig. 9); male with hooked tooth on anterior margin of chelicerae (Figs. 5-8); tip of the embolus not coiled (Figs. 9-11); New Jersey*heleios*
 Paracymbium without a tooth in its anterior margin3
- 3. Female unknown; male with hooked tooth on anterior margin of chelicerae (fig. 285); tip of embolus coiled (fig. 289); Mississippi (map 8)*iviei*
 Male without hooked tooth on anterior margin (fig. 276); tip of embolus not coiled (fig. 280); southern Canada to Central America, West Indies (map 8)*foxi*

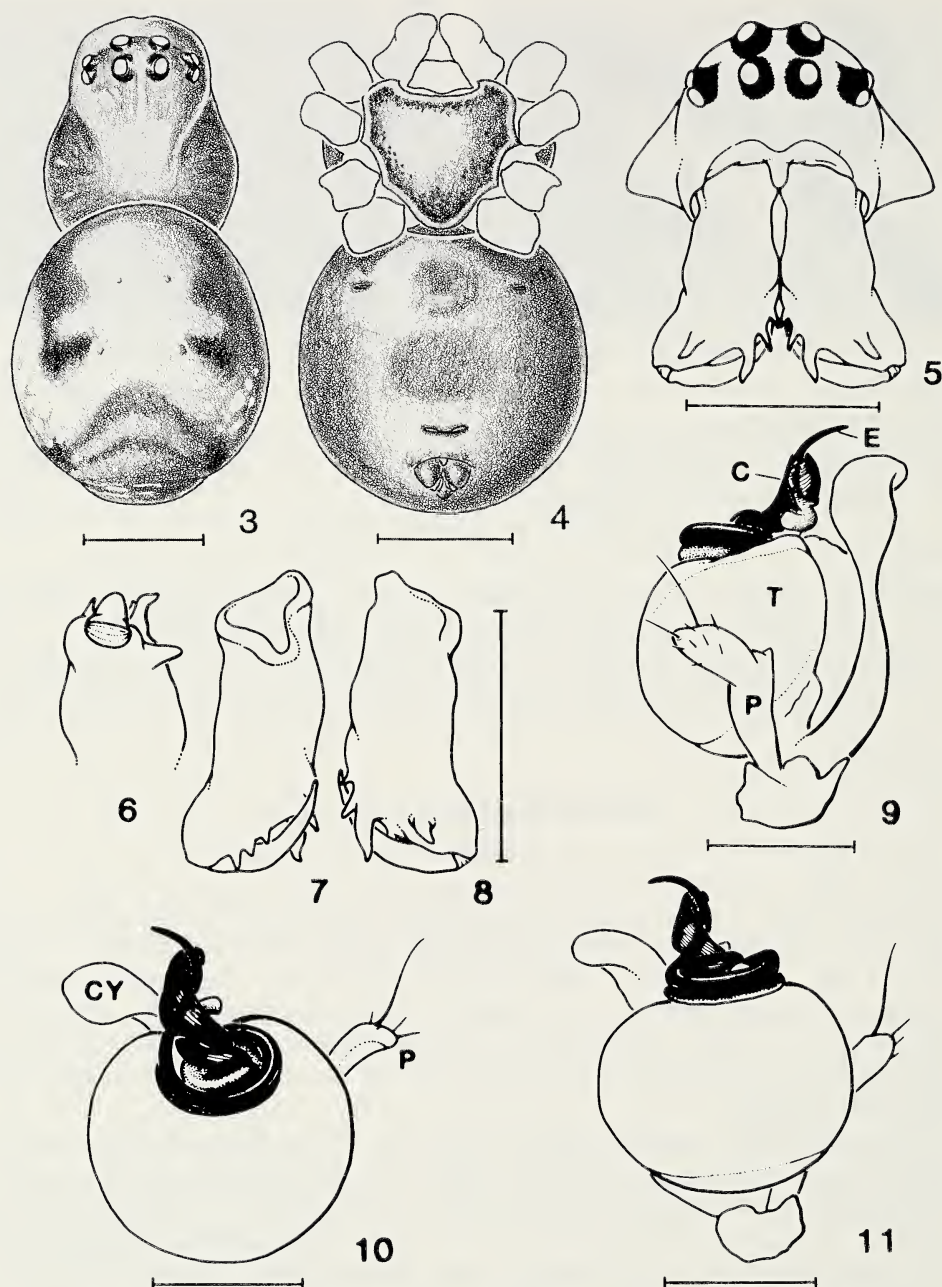
Glenognatha heleios, new species
 Figures 1-17

Types.—Male holotype, four male paratypes and three female paratypes from New Jersey, Ocean Co., Tuckerton; collected on *Spartina alterniflora* in a lightly flooded salt marsh; 7 Nov. 1984 (8-1) (H. Döbel col.). Eight male and eight female paratypes from the same locality; 9 Oct. 1984 (8-2) (H. Döbel col.). Deposited in USNM; paratypes are also deposited in AMNH and MCZ. For nomenclatural purposes the senior author should be considered the author of the species description.

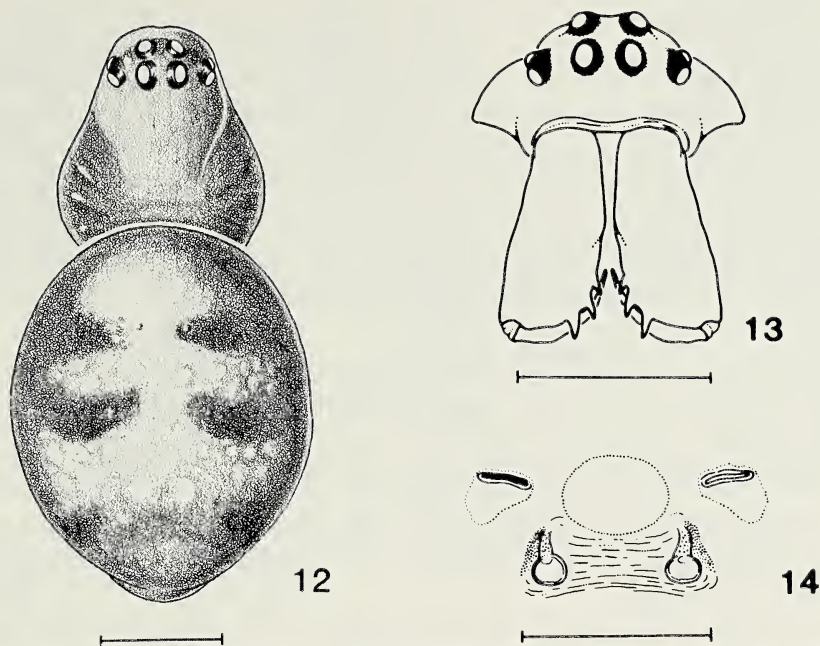
Etymology.—The specific epithet is from the Greek *helos* (marsh, meadow), hence *heleios* dwelling in a marsh, and refers to the known habitat of this species.

Diagnosis.—*Glenognatha heleios* differs from *G. iviei* Levi, 1980 in the shape of the paracymbium and the presence of a tooth on its anterior margin (Fig. 9). The larger body size and the shape of the hooked tooth on the chelicerae also separate *G. heleios* from *G. iviei* (Figs. 5-8).

Description.—Male (Holotype). Total length 2.04. Cephalothorax 1.03 long, 0.87 wide, 0.65 high. Sternum 0.50 long, 0.53 wide. Abdomen 1.25 long, 1.06 wide, 0.93 high. AME diameter 0.063; eyes of equal diameter; AME separation 1.25 times their diameter, PME separation 1.25 times their diameter; ALE, PLE juxtaposed; PME-PLE separation 1.75 times one PME diameter. Clypeus height 3.5 times one AME diameter. Chelicerae large (Figs. 5-8), four prolateral and four retrolateral teeth. Cephalothorax, chelicerae, sternum and legs light brown. Abdomen (Fig. 3, 4), dorsum light gray with black and white dorsal marks;



Figures 3-11.—*Glenognatha heleios* n. sp.: 3-5, holotype male; 3, dorsal; 4, ventral; 5, eye region and chelicerae; 6-8, left chelicera of male paratype; 6, distal portion, ectal; 7, posterior; 8, anterior; 9-11 palp of holotype male; 9, mesal; 10, posteroectal; 11, ectal. Abbreviations: C = conductor; CY = cymbium; E = embolus; P = paracymbium; T = tegulum. Scale bars: 0.5 mm for Figs. 3-8, 0.25 mm for Figs. 9-11.



Figures 12-14.—*Glenognatha heleios* n. sp., paratype female; 12, dorsal; 13, eye region and chelicerae; 14, genitalia, dorsal. Scale bars: 0.5 mm.

venter dark gray with light marks. Leg and pedipalp lengths of male described above:

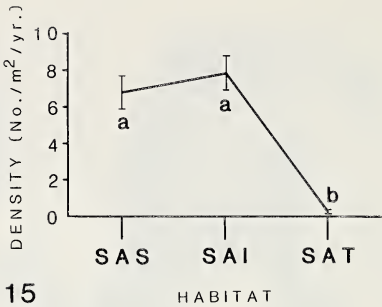
	Fe	Pt	Ti	Mt	Ta	Total
I	1.12	0.34	1.12	0.87	0.53	3.98
II	1.03	0.34	0.97	0.81	0.47	3.62
III	0.65	0.28	0.47	0.47	0.31	2.18
IV	0.90	0.28	0.78	0.65	0.40	3.01
Pdp	0.47	0.19	0.12	—	0.59	1.37

Legs I>II>IV>III. Palp (Figs. 9-11).

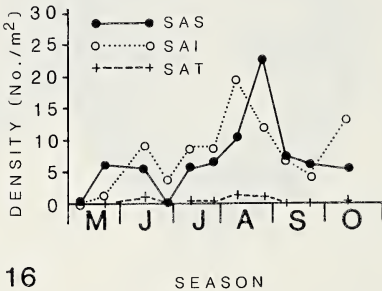
Female (Paratype).—Total length 2.39. Cephalothorax 0.97 long, 0.84 wide, 0.65 high. Sternum 0.53 long, 0.59 wide. Abdomen 1.56 long, 1.25 wide, 1.25 high. AME diameter 0.063; eyes of equal diameter; AME separation 1.25 times their diameter, PME separation 1.25 times their diameter; ALE, PLE juxtaposed; PME-PLE separation 1.25 times one PME diameter. Clypeus height 2.4 times one AME diameter. Chelicerae (Fig. 13), three prolateral and three retrolateral teeth. Cephalothorax, chelicerae, sternum and legs light brown. Abdomen (Fig. 12), dorsum light gray with black and white marks, venter dark gray. Leg and pedipalp lengths of female described above:

	Fe	Pt	Ti	Mt	Ta	Total
I	1.02	0.31	0.90	0.84	0.50	3.57
II	0.93	0.31	0.81	0.68	0.47	3.20
III	0.65	0.25	0.43	0.47	0.50	2.30
IV	0.90	0.28	0.68	0.62	0.37	2.85
Pdp	0.31	0.12	0.25	—	0.25	0.93

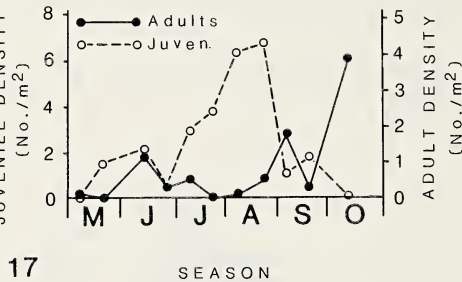
Figures 15-17.—*Glenognatha heleios*, seasonal abundances at Tuckerton, New Jersey; 15, annual mean densities (no./m²/yr) in the three *Spartina alterniflora* habitats along an elevational gradient. Means (\pm SE, $N = 22$) with different letters are significantly different $P < 0.05$; 16, seasonal abundance (no./m²) in the three *Spartina alterniflora* habitats. Plotted are the means of two plots for each habitat sampled on 11 dates from 7 May to 11 October 1985; 17, seasonal abundance (no./m², average across all habitats) of adults and juveniles. Abbreviations: SAS, short form *S. alterniflora*; SAI, intermediate form *S. alterniflora*; SAT, tall form *S. alterniflora*.



15



16



17

Legs I>II>IV>III. Vulva (Fig. 14).

Variation.—Male cephalothorax length ranges from 1.00 to 1.15 ($n = 13$), females from 0.90 to 1.03 ($n = 9$). Specimens in alcohol vary in abdominal pattern, with darker pigmentation of the dorsal pattern and more pronounced chevron marks in the posterior part of the abdomen; other specimens lack such marks. The dorsal white silver spots vary in size and number. In some specimens the abdominal pattern is hardly visible.

Natural history.—In general, *G. heleios* occurred at rather low densities, averaging six to eight individuals per m² each season. This species was most abundant in short and intermediate form *Spartina alterniflora* and very rare in tall form *Spartina* (Fig. 15). Peak densities of about 25 individuals per m² were reached in July/August (Fig. 16). In New Jersey *G. heleios* is a univoltine species producing juveniles from July to August followed by an adult peak in mid-October (Fig. 17). This species overwinters in the adult stage.

Webs were only found in the short and intermediate form of *Spartina alterniflora* where the amount of tidal flooding is very low (<0.5 cm). The web is located very close to the soil surface (1 to 5 cm) and oriented horizontally. The

sticky spiral is very closely spaced, leaving only minute gaps between two successive turns of the thread (Fig. 2).

Distribution.—*G. heleios* has been recorded only from a single locality, an intertidal salt marsh near Tuckerton, New Jersey where extensive sampling took place (Döbel et al. in prep.). Nevertheless it is likely that this species also will be found in other salt marshes with similar habitat structure and climatic pattern.

Material examined.—New Jersey: Ocean Co., Tuckerton; *S. alterniflora* salt marsh, lightly flooded (H. Döbel col.); 28 Aug. 1984 (8-4), 3 males; 25 Sep. 1984 (1-2), 2 males; 9 Oct. 1984 (8-4), 3 males; 7 Nov. 1984 (14-1), 4 males, 2 females; 7 Nov. 1984 (8-2), 3 males, 3 females; 7 Nov. 1984 (14-4), 3 males, 4 females; 11 Nov. 1984 (14-4), 4 males, 3 females. Deposited in USNM.

Glenognatha centralis Chamberlin, 1925
Figures 18-24

Glenognatha centralis Chamberlin, 1925: 216 (Male description, not illustrated). Female unknown.

Type.—Male holotype, label states “*Glenognatha centralis* Chamb. Male Holotype Panama (B. 1072) R. V. Chamberlin Coll.” Deposited in MCZ, examined.

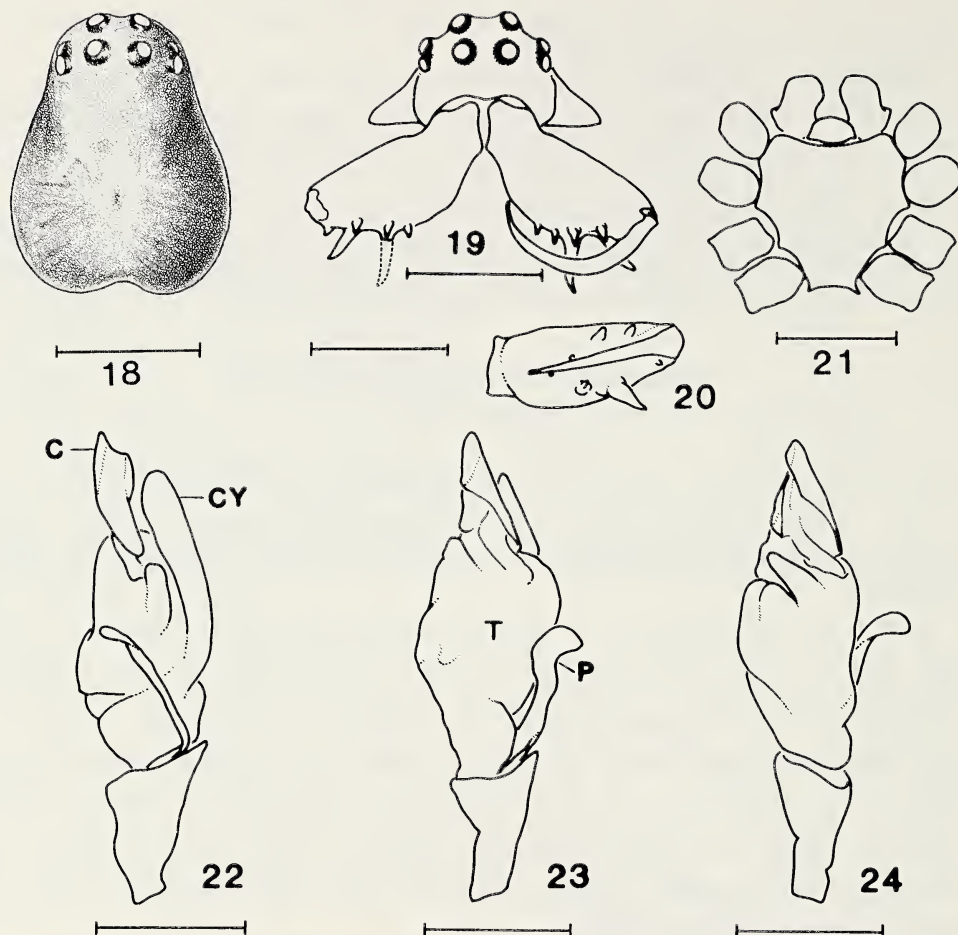
Note.—The type material of *G. centralis* (collected from the stomach of a toad, *Bufo* sp.) is in bad condition, missing many of the legs and the right pedipalp. The palpal characters are difficult to see because its morphology is distorted, probably due to the digestion process. The embolus is missing. We are not even sure whether the type material represents an adult or is a subadult before the last molt. After comparison with other Panamanian *Glenognatha* from the MCZ collection we have not found any specimen that matched *G. centralis* in any characters known to be useful for species diagnosis in *Glenognatha*. Therefore the description and diagnosis has to be based on this single specimen until new specimens are available for study.

Diagnosis.—*G. centralis* chelicerae (Fig. 19) are much more divergent than those of the other Central and North American species, and this divergence does not seem to be an artifact of preservation. The tegulum appears to be smaller than in other species of *Glenognatha* and the conductor shape seems unique to this species, being more elongated and its position more apical (Figs. 22-24).

Description.—Male (Holotype). Cephalothorax 0.97 long, 0.81 wide, 0.81 high. Sternum 0.53 long, 0.59 wide. AME diameter 0.156; eyes of equal diameter; AME separation one time their diameter, PME separation one time their diameter; ALE, PLE juxtaposed; PME-PLE separation 1.4 times one PME diameter. Clypeus height 2.2 times one AME diameter. Chelicerae large and strongly divergent (Figs. 19-20), three prolateral and four retrolateral teeth. Cephalothorax, chelicerae and sternum brownish, legs slightly lighter. Leg and pedipalp lengths of male described above:

	Fe	Pt	Ti	Mt	Ta
III	0.78	0.28	0.59	—	—
IV	1.09	0.34	0.87	—	—
Pdp	0.56	0.22	0.22	—	0.40

Palp (Figs. 22-24).



Figures 18-24.—*Glenognatha centralis* Chamberlin, holotype male; 18, carapace, dorsal; 19, eye region and chelicerae; 20, left chelicera, ventral; 21, sternum and coxae; 22-24, palp; 22, dorsal; 23, ectal; 24, ventral. Scale bars: 0.5 mm for Figs. 18-20; 0.25 mm for Figs. 22-24.

Distribution.—Only known from Panama (locality not specified in the label).

Material examined.—Only the holotype.

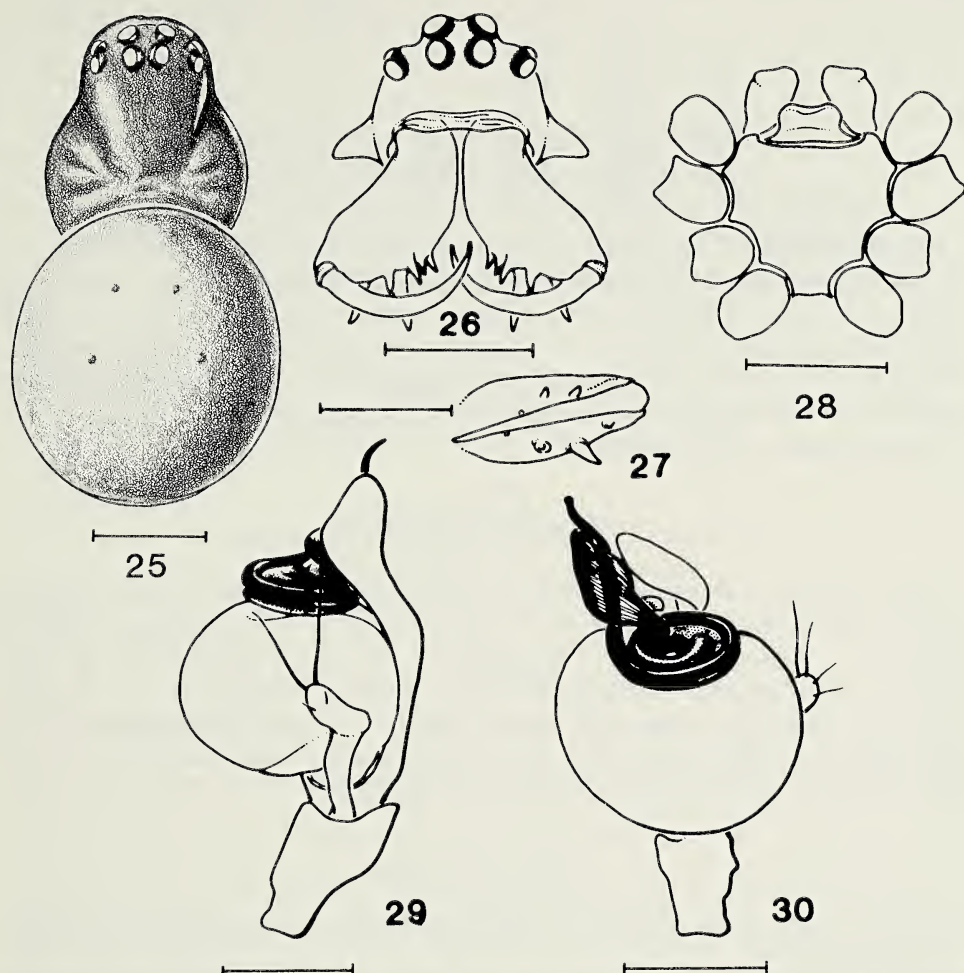
Glenognatha minuta Banks, 1898

Figures 25-30

Glenognatha minuta Banks, 1898: 248, pl. XV, fig. 15 (male lateral view and chelicera), female unknown.

Type.—Male syntype, labels state “*Glenognatha minuta* Bks Cotype San Jose del Cabo, Baja Calif. Eisen & Vaslit.” and “Nathan Banks Coll.” Deposited in MCZ.

Note.—*G. minuta* was described after two specimens, but no holotype was designated. The syntype series belonged to the California Academy of Sciences although Banks kept duplicate specimens. After the destruction of the specimens at the California Academy of Sciences during the earthquake in 1906 only the



Figures 25-30.—*Glenognatha minuta* Banks, syntype male; 25, dorsal; 26, eye region and chelicerae; 27, left chelicera, ventral; 28, sternum and coxae; 29, 30, palp; 29, mesal; 30, dorsoectal. Scale bars: 0.5 mm for Figs. 25-28; 0.25 mm for Figs. 29, 30.

duplicates have been available for study (Levi, pers. comm.). Therefore, although only one specimen survived, it should be considered as syntype. It does not seem appropriate to designate a lectotype.

Diagnosis.—*G. minuta* differs from other *Glenognatha* species in the shape of the embolus and the conductor (Figs. 29, 30). It also differs from other North American species by the cheliceral teeth (Fig. 26, 27).

Description.—Male syntype. Total length 2.28. Cephalothorax 1.15 long, 0.90 wide, 0.87 high. Sternum 0.56 long, 0.62 wide. Abdomen 1.37 long, 1.19 wide, 1.15 high. AME diameter 0.095; PME 0.83, PLE 0.83, ALE 0.83 times one AME diameter; AME separation one time their diameter, PME separation 1.4 times their diameter; ALE, PLE juxtaposed; PME-PLE separation 1.8 times one PME diameter. Clypeus height two times one AME diameter. Chelicerae large (Figs. 26, 27), three prolateral and four retrolateral teeth. Cephalothorax, chelicerae and sternum red-brown, legs light brown. Abdomen very light brown, no pattern visible. Leg and pedipalp lengths of male described above:

	Fe	Pt	Ti	Mt	Ta
I	1.56	0.56	1.53	—	—
II	1.50	0.34	—	—	—
III	1.03	—	—	—	—
IV	1.37	0.31	1.09	—	—
Pdp	0.59	0.22	0.22	—	0.56

Palp (Fig. 29-30).

Distribution.—Recorded from Baja California (San José del Cabo, type locality). Bryant (1940:358) misidentified a specimen from Cuba as *G. minuta*. The Cuban specimen belongs to a different species which has a longer embolus, thinner at its end and more curved. Its paracymbium is also different as Bryant noticed, with the basal part being wider than in the type specimen.

Material examined.—Only the syntype.

ACKNOWLEDGMENTS

Type material and other specimens were kindly provided by the following curators and institutions (acronyms in parentheses): J. A. Coddington, National Museum of Natural History, Smithsonian Institution (USNM); H. W. Levi, Museum of Comparative Zoology, Harvard University (MCZ) and N. I. Platnick, American Museum of Natural History (AMNH). We are also grateful to J. A. Coddington for helpful comments and constructive criticism, and to H. W. Levi and C. Mitter for reviewing an earlier draft of this paper.

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**EARLY STAGES OF ORB CONSTRUCTION
BY *PHILOPONELLA VICINA*,
LEUCAUGE MARIANA, AND *NEPHILA CLAVIPES*
(ARANEAE, ULOBORIDAE AND TETRAGNATHIDAE),
AND THEIR PHYLOGENETIC IMPLICATIONS**

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ABSTRACT

The uloborid *Philoponella vicina* differs from the araneoids *Nephila clavipes* and *Leucauge mariana* in one movement made during frame construction, in the ordering of frame construction, in proto-hub removal, and in the highly ordered sequence of operations on adjacent radii just before proto-hub removal. Data from other uloborids suggest that all of these differences may distinguish orb weaving uloborids in general from orb weaving araneoids. *N. clavipes* differs from the other two species in the order of lines laid during frame construction, in the high variability in the details of frame construction, and in its failure to remove recently laid lines during exploration, radius construction, and frame construction. Frame construction behavior in all three species is more variable than previous reports indicated, and more variable than behavior in later stages of orb construction. In all three species earlier frame construction more often involves breaking lines already present in the web.

Similarity between uloborid and araneoid frame construction is more likely to be due to a combination of constructional constraints and inheritance of ancient spinning patterns than previously realized; it is not clear whether or not it constitutes a synapomorphy uniting the two groups. The failure of *N. clavipes* to remove recently laid lines during exploration, radius construction, and frame construction is probably plesiomorphic. Secondary loss of removal behavior seems unlikely because removal probably confers adaptive advantages. Removal behavior in these contexts and possibly more stereotyped frame construction behavior probably evolved independently in uloborids and araneoids.

INTRODUCTION

The question of whether orb webs evolved once or more than once independently in uloborid and araneoid spiders has long been controversial (see Coddington 1986a and Shear 1986 for recent reviews, also Kooor and Peters 1988). Perhaps the strongest evidence favoring the single origin hypothesis is that both the basic construction processes and the sequence in which they occur are similar in both groups (e.g., Wiehle 1927). Since similarities in later stages of orb construction could result from the patterns of lines produced during earlier stages, the earlier stages of orb construction are especially important for arguments of monophyletic origin. These stages, however, are the least studied and most poorly understood parts of orb construction behavior.

Part of the reason for our ignorance is that initiation of orb construction is more difficult to study than later stages: behaviors are not repeated as many times per web; lines and attachments are often displaced substantially by subsequent behavior (e.g., Tilquin 1942), making it difficult for an observer to maintain an accurate frame of reference; the spiders seem more sensitive to disturbances (Koenig 1951; Witt et al. 1968; Vollrath 1986); and construction of the first series of lines often involves long pauses (sometimes over an hour) (Witt et al. 1968). Arachnologists have had difficulty describing the early stages of web construction. For instance, there are many published descriptions of frame construction which are probably simply wrong (McCook, 1889; Hingston 1920; Comstock 1940; Savory 1952; Levi and Levi 1968; Dugdale 1969; Forster and Forster 1973; Levi 1978; Foelix 1982—see Tilquin 1942 and discussion of this paper); with the possible exception of Tilquin 1942, all other accounts (Peters 1933; Koenig 1951; Mayer 1952; Eberhard 1972; Coddington 1986a) are probably flawed in ignoring variations.

This paper reports detailed observations of the early stages of web construction by the uloborid *Philoponella vicina* (O. Pickard-Cambridge) and the tetragnathids *Leucauge mariana* (Kersterling) and *Nephila clavipes* (Linnaeus). It also gives brief descriptions of the behavior of four other uloborids, even briefer notes on that of a variety of other tetragnathids and araneids, and summarizes all published observations of certain aspects of uloborid behavior which appear to be unique to this group. The impact of these data on the single vs. multiple origin of orb controversy is then discussed.

METHODS

P. vicina and *N. clavipes* normally build between midnight and 0800 hours, so adult females of *P. vicina* and nymphs of *N. clavipes* (probably 2nd-6th instars) were kept in a small light-tight shed (about $3 \times 3 \times 2$ m) in which lights were turned on at 1400 hours and shone until 0500. A partially shaded 50 W bulb was kept burning at all times in order to increase the spiders' tolerance of light during the dark phase (Eberhard 1972).

Webs of *P. vicina* in the field were taped to a 25 cm diameter wire hoop; with the spider still in place, each was suspended horizontally in the shed. The spiders' behavior was observed as they built subsequent webs in the hoops. *N. clavipes* were induced to build webs on wire frames, which varied from 20-40 cm in diameter according to the size of the spider, by isolating the spider from contact with other surfaces by placing the frames in covered pails containing a little water. Both species were observed by lighting the background with a headlamp and watching their silhouettes, by shining the headlamp on the spider from the side and above, or by watching the spider against a surface illuminated by the 50 W bulb. Except when the headlamp shone upward from less than about 20 cm below the spider (a position avoided during the observations), it seldom caused overt disturbance of the spider (as indicated by interruption of building, bouncing on the web, or clear disorientation of behavior).

Observations of *N. clavipes* were especially difficult to record because the spiders' behavior was highly variable, so they were recorded verbally on a tape recorder, then later transcribed. To avoid startling the spider when I began to speak, a radio was played softly during the entire building period.

Mature female *L. mariana* were kept on horizontal wire hoops in an outdoor screen cage as described in Eberhard 1987a, and were observed late in the morning and early in the afternoon while they made their second complete webs of the day. These spiders moved much more rapidly, but their large size and the better viewing conditions made detailed observations possible.

The starting point of construction was standardized by cutting away most of the previous web that was present at the beginning of an observation period, using a scissors or a hot, fine-tipped soldering iron to leave only three long radial lines diverging from the web's previous hub. The mesh lines of *N. clavipes* outside the plane of the orb were generally left more or less intact. To assure that *P. vicina* and *L. mariana* webs were horizontal, any lines that the spider laid out of the plane of the hoop were cut just after they were laid.

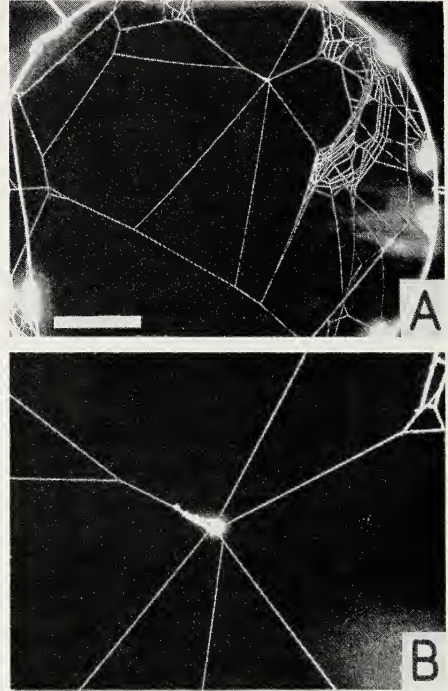
My observations were somewhat prejudiced against unusual behavior patterns, because I was unable to record behaviors in which I did not understand the sequence of line placements and removals; "standard" patterns were easiest to understand because I could anticipate the spider's movements. The number of "standard" behaviors I recognized increased during the study, and toward the end I was seldom unable to understand any *P. vicina* or *L. mariana* behavior. However, mesh construction by *N. clavipes* was so variable and complex that I was often unable to describe a spider's behavior, even at the end of the study. Orb construction in this species was much more stereotyped than mesh construction, but was still substantially more variable than that of the other species, and new sequences were seen even at the end of the study.

Construction of over 60 *P. vicina* webs, 60 *L. marina* webs and 35 *N. clavipes* webs was observed (6 of the *N. clavipes* webs were small "resting" webs without sticky spirals). Because I did not note all aspects of building behavior for each web, separate sample sizes are given for each behavior. In the latter part of the study I recorded complete lists of the directions and orders of placement of frames and radii in 17 *P. vicina* and 18 *L. mariana* webs, starting observations soon after the spider began sustained activity. These webs are called "study" webs in the text. The order of the spider's operations in each of these webs was later coded by counting back from the last radius laid in the web; in *P. vicina* I also counted the number of behaviors before and after proto-hub replacement. The position of a given behavior in the entire sequence is indicated in relation to the total number (N) of radii laid in the web (i.e., the last radius is $1/N$, the next-to-last is $2/N$, etc.). These fractions probably make some behaviors appear to have occurred earlier in the construction sequence than they actually did, since the totals do not include very early behaviors that were followed by long pauses.

The behavior of *Uloborus trilineatus* (Kersterling) was observed as in *P. vicina*, while all other species were observed in the field.

Unless otherwise noted, all statistical tests were made with Chi-squared Tests. Averages are followed by \pm standard deviations. The figures which describe behavioral sequences are stylized summaries, and are not to scale. The behaviors observed are classified (e.g., radius construction, frame construction, mesh construction) on the basis of the web lines which were laid as a result of the behavior. Hub construction consisted of laying more or less circular lines at the hub which were attached to all or nearly all of the radii that were crossed.

Figure 1.—Web of *Philoponella vicina*: A, nearly complete proto-web; B, closeup of the proto-hub, showing large accumulation of loose silk and lack of hub lines connecting radii.



RESULTS

***Philoponella vicina*.**—The following sequence summarizes the early stages of web construction. Initial “exploration” changed more or less gradually into construction of the radii and frames of the proto-web (Fig. 1). Then the spider always removed the center of this web ($N = 37$) (proto-hub removal or PHR) reconnecting the radii as it did so (Fig. 2). Following PHR, the spider began laying hub spiral, and laid more radii and sometimes more frames. These stages are described in detail below.

I. Exploration: The earliest portions of behavior, corresponding to the “exploration” stage of Eberhard (1972), were especially difficult to observe and describe, and I was unable to perceive overall patterns. Several details were the same as those of *U. diversus* (Eberhard 1972). Descents occurred both on the end of a single line, and while the spider spanned a broken line with its body, reeling in one broken end while paying out dragline silk that was attached to the other. Often descents on broken lines began with the spider paying out line faster than it reeled it in, and ended with it reeling in more rapidly than it paid it out. This caused the spider to descend through an arc, then climb more or less straight up. Some descents on single lines were preceded by two to four increasingly deep descents back and forth on the same radial line, but others were not. Spiders sometimes descended >50 cm to touch the floor, then immediately reascended the dragline without making an attachment. The failure to attach suggests that this behavior functions as exploration. Spanning lines carried on air currents (Eberhard 1987b) were often initiated on descents, but spiders did not usually move far from the original website.

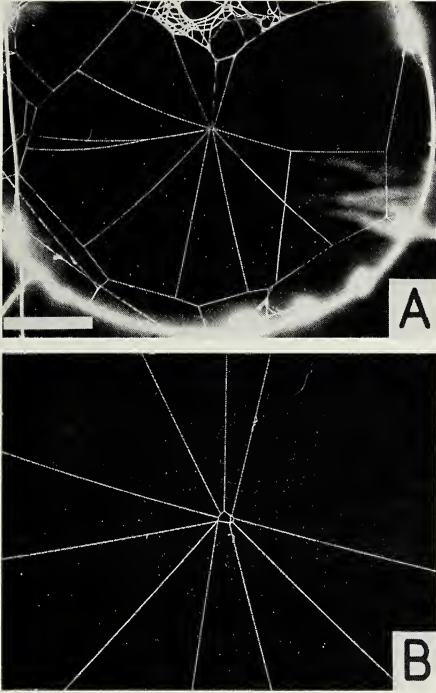


Figure 2. Web of *P. vicina*: A, just after protohub replacement (one radius was laid after the protohub was removed); B, closeup of hub of this web. The loose silk is gone, and the radii are connected by an approximately circular line that was laid as the loose silk was removed.

Spiders moved lines by breaking them at one end, and spanning the hole while carrying the broken end to another attachment site (Eberhard 1972). Similar results were achieved by removing a line entirely and replacing it with a new dragline that was attached at a different point. Accumulations of silk from previous webs were sometimes cut free and discarded with waving movements of legs I; other accumulations were cut free, wrapped for several minutes, and ingested as described for *U. diversus*. The reason some silk was discarded is unclear. Two spiders which dropped an accumulation of silk while removing lines from previous webs later ingested turfts of newly laid silk at the proto-hubs of the same webs.

The length of time spent in exploration varied greatly, and activity was often interrupted by pauses of an hour or more. Eventually several lines were joined together approximately where the future hub would be (the "proto-hub") (Fig. 2). Sometimes there were two such sites of intersection, and one was later removed or moved and added to the other.

Attachments to the wire rim were generally made on a surface of the wire that faced somewhat away from the direction of the line itself. This probably results in a firmer attachment to the substrate, since (other things being equal) the force exerted by the line on the attachment will be more nearly parallel to the plane of the attachment (compare the difficulty of pulling an adhesive tape directly off of a surface versus sliding it along the surface).

II. Frame construction and events leading up to PHR: The behavior immediately preceeding PHR became less variable. Radial lines were "modified" in one of three ways: moved; removed partially or completely; or connected by frames. Two kinds of partial replacements occurred. In the simplest and most common (124 of 126 cases in which this detail was recorded in the study webs),

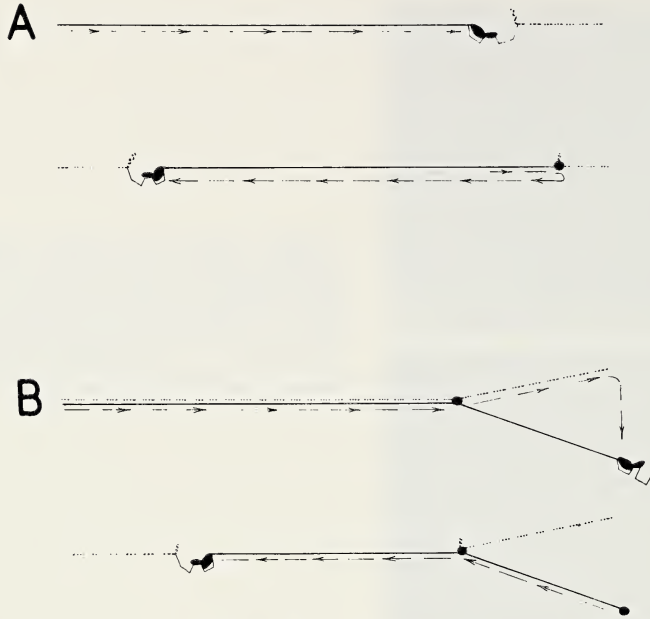


Figure 3.—Two types of partial replacement of radii: Dashed lines with arrows show the route taken by the spider's feet, dotted lines are lines already present, intact lines are those newly laid in each drawing, and large dots mark new attachments. A, the spider breaks and reels up the exit radius while moving away from the hub (above), then turns and replaces the newly laid dragline by breaking and reeling on the way back (below); B, the spider leaves the exit line intact as it leaves the hub, attaches its dragline to the exit on the way out and then moves onward and sideways (above). After making an attachment to the substrate or other lines, it returns, replacing the newly laid dragline and its attachments to other lines with another dragline and attachments (below).

the spider broke the exit radius while moving away from the proto-hub as just described. It stopped part way out the exit, turned 180° and attached the dragline to the outer broken end, then returned to the hub reeling up the dragline it had just laid (Fig. 3A). In a few cases (2 in the study webs) the exit radius was left intact on the trip out, the dragline was attached to it part way out and the spider continued onward and to the side without breaking the exit line (in one case it broke other lines it encountered there). After attaching the dragline, the spider returned to the hub, reeling up and replacing both the exit line and the line that it had laid on the way out (Fig. 3B).

Spiders also often moved radii by replacing them (56 of 186 cases in which radii were modified in study webs; 63% of the 56 involved frame construction). The spider began as if to replace the radius, breaking the line (the "exit radius") at the proto-hub or while moving away from the proto-hub and rolling up the loose silk as it went. It moved all the way to the end of the exit, then moved to one side along other lines or the wire rim, sometimes cutting other lines in the vicinity and/or attaching the dragline one or more times to them. Then it attached the dragline and turned back to return along it to the proto-hub, reeling up and replacing the newly laid line. The spider attached the new dragline at the hub, but did not generally make any other attachments before leaving on another trip away from the hub.

Sometimes (8 times in 17 study webs) the spider added a new radius: it moved away from the proto-hub without breaking the exit line, and then moved to the

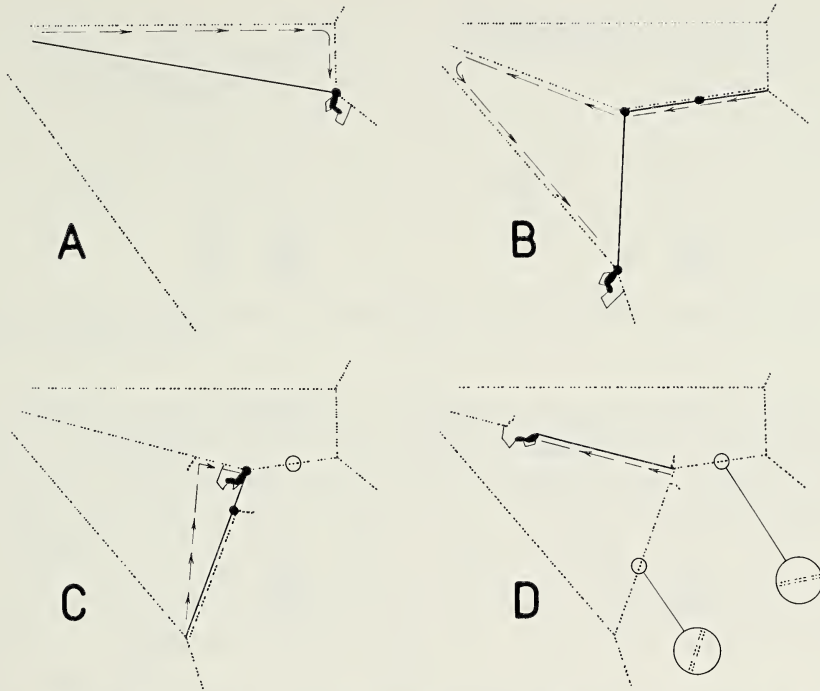


Figure 4.—Sequence of events in *P. vicina* frame construction Type A (conventions as in Fig. 3): Lines already present during a given stage are all represented as being single. Insets here and in later figures are included to clarify the number of “lines” actually present (in fact, spiders generally lay a pair or more of lines as they move; each line in the insets represents all of the components of a single dragline).

side, away from the end of this radius, attached its dragline to the frame line or wire rim, and returned to the hub along the new radius, breaking it and rolling it up as it went. This sequence of behavior was identical to the typical radius construction behavior of araneoids (F1 of Eberhard 1982). Addition of radii was probably more common than the numbers suggest since the very earliest stages of construction that were followed by long pauses were not counted. One radius (laid just before PHR) was sealed by the spider on its way to the hub (Fig. 8).

Frame construction behavior varied (types A-E in Figs. 4-8), but several details showed clear patterns. On the first trip back to the hub spiders sometimes attached to the exit radius twice instead of once as shown in Fig. 5B. Spiders always broke the second portion of the new frame line while returning to the new radius, and always shifted the attachment outward (e.g., Fig. 4C) before returning to the hub ($N = 126$) (Figs. 4-8). In four cases the new frame (e.g., the line laid in Fig. 4C) was slack and the spider reeled in part of the line with its legs IV, thus tightening it before attaching to the radius. The tuft of loose silk that accumulated as the spider returned from each frame construction and radius replacement was left along with other similar tufts at the proto-hub.

Frame construction behavior B (Fig. 5) was most common (44 of 70 cases in study webs); D (Fig. 7) was next (12 of 70), then A (Fig. 4) (9 of 70), C (Fig. 6) (3 of 70), and E (Fig. 8) (2 of 70). All A and B frame constructions occurred before PHR, all D came after PHR (D differs from A and B with respect to occurrence before or after PHR, $P < 0.01$); 2 of 3 C occurred before PHR).

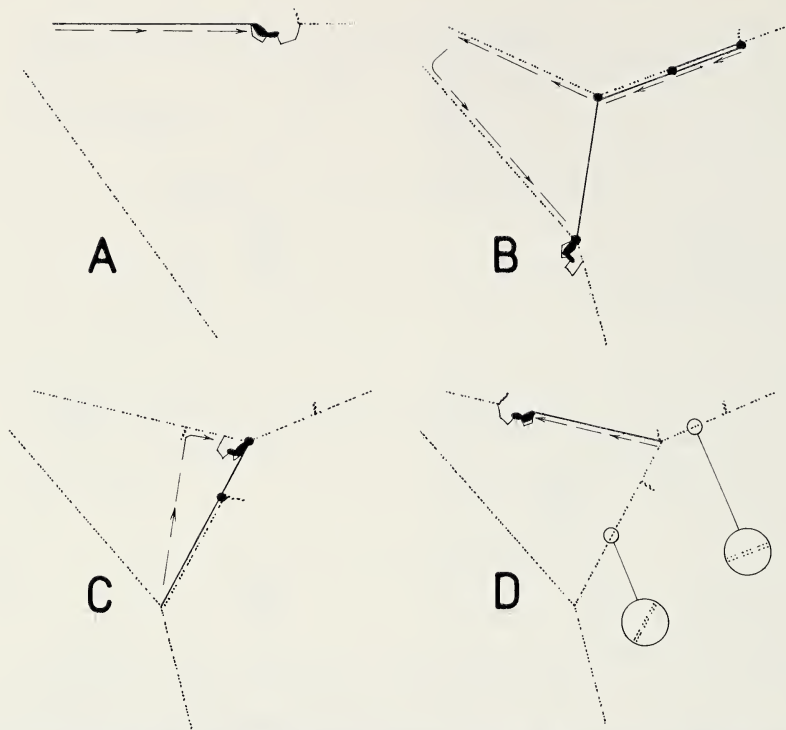


Figure 5.—Sequence of events in *P. vicina* frame construction Type B (conventions as in Figs. 3 and 4).

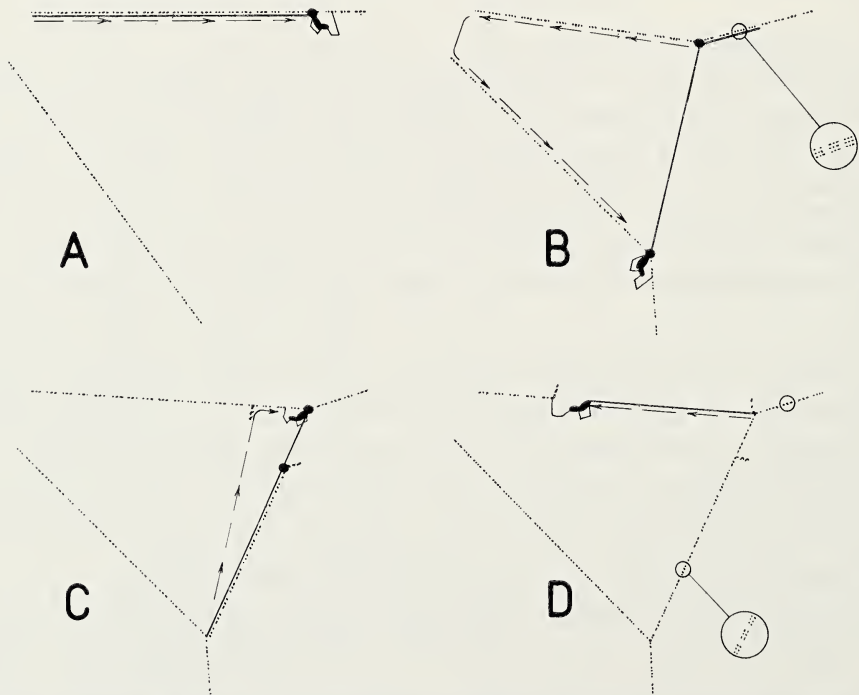


Figure 6.—Sequence of events in *P. vicina* frame construction Type C (conventions as in Figs. 3 and 4).

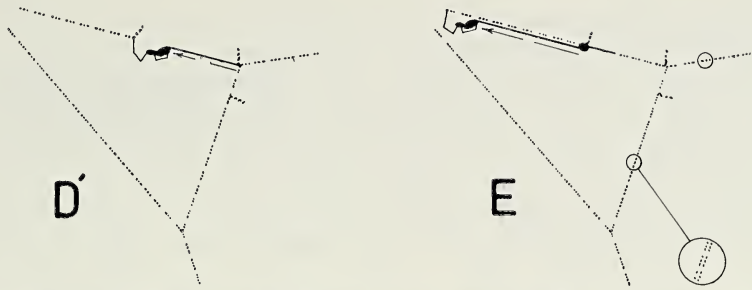


Figure 7.—Sequence of final events in *P. vicina* frame construction Type D (stages A-C as in Fig. 6) (conventions as in Figs. 3 and 4).

The impending approach of PHR was signalled when the spider modified radii (partially or completely replaced them or added frame lines) one after another in strict sequence moving around the web. An example of such a sequence was a spider which began this stage with radii at 1, 2, 3, 5, 6, 7, 9 and 10:00 positions.. First it modified the 9:00 radius, then, in order, those at 7, 6, 5, 3, 2, 1, and 10:00. In 30 webs in which positions of modified radii were noted, the last five modifications on radii preceding PHR were all on adjacent radii and all progressed in a consistent direction except for two cases in which the spider skipped a single radius.

In addition, when the direction in which a frame line was laid was noted ($N = 50$), the frame was always laid so that the exit radius was on the "leading" or far

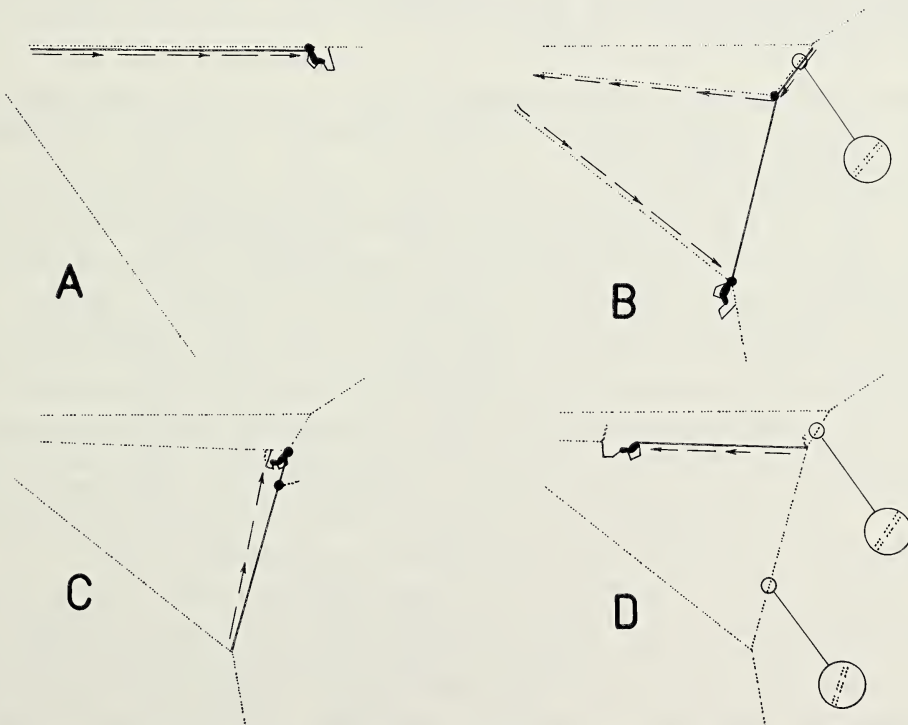


Figure 8.—Sequence of events in *P. vicina* frame construction Type E (conventions as in Figs. 3 and 4).

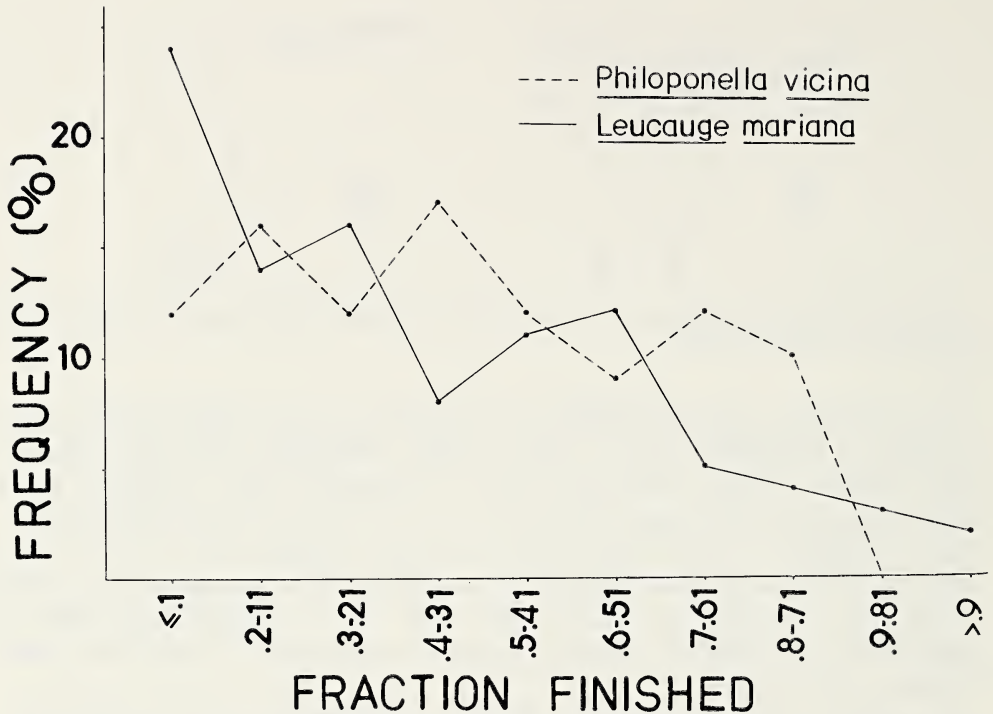


Figure 9.—Relative numbers of frame lines built at different stages of orb construction by *P. vicina* (dotted line) ($N = 58$ frames in 17 orbs) and *L. mariana* (solid line) ($N = 92$ frames in 18 webs) (stage of construction indicated by fraction of final number of radii already present). Since some observations began after the first few radii had been laid (inset in Fig. 15), the frames laid in the very earliest stages (< 0.20) are under-represented.

side of the sector that would be spanned. Thus in the web just mentioned, the exit on the 9:00 radius resulted in a frame connecting 9 to 10, that on 7 resulted in a frame from 7 to 9, etc.

The last behaviors preceding PHR tended to result in smaller modifications of the web. The last modification before PHR was more likely to be a partial replacement than a frame construction or radius shift ($P < 0.01$ comparing last modification before PHR with preceding five in 27 webs). In addition, the partial replacements performed during one or two radial modifications just preceding PHR ($N = 24$ in study webs) more often involved only the inner 20% portion of the radius' length than those performed earlier ($N = 54$) ($P < 0.01$).

III. Proto-hub removal (PHR): The spider simultaneously cut the accumulation of loose silk free from where the radii converged, ingested it, and reattached the radii. In some, but not all cases, the new line joining the radii was nearly circular (Fig. 2). In 13 webs which had an average of 17.7 ± 4.4 radii when finished, an average of 7.3 ± 2.1 radii were present when the proto-hub was removed.

IV. After PHR: Following PHR, the spider added new radial lines as well as occasional frames (Fig. 9). Usually the spider chose to exit along the leading edge of a sector (100 of 127 in 31 webs) as in frame construction preceding PHR, but in other respects the behavior was quite different. Existing radii were seldom replaced following PHR (7 of 176 trips from away from the hub in the study webs). Hub spiral construction after each trip away from the hub began abruptly, usually and perhaps always starting with the first radius after PHR (occasionally

it was difficult to be sure of this point for the first new radius or two). All new radii were added without breaking lines, as described in Eberhard 1972 and 1982 (character F3), and radial lines were continuous with the hub spiral. Frame construction differed from that preceeding PHR; it did not involve breaking previous lines on the way out from the hub, and it included sealing the break in the new radius part way back to the hub (types D and E—see Figs. 7 and 8).

Leucauge mariana.—Nothing corresponding to PHR was ever performed by *L. mariana* in the early stages of construction. Unless otherwise noted, all data are from the study webs.

I. Exploration: As with *P. vicina* (and *Araneus diadematus*—Reed 1968), preliminary placement and removal of lines prior to construction proper was generally carried out intermittently over several hours. The same behaviors were used, including breaking and reeling while replacing lines, shifting attachment points of lines, descent on single lines (often reaching objects below the web without making an attachment), and production of airborne spanning lines. The only exploratory *P. vicina* behavior not performed by *L. mariana* was wrapping of accumulated loose silk from the previous web; this difference was not surprising since the very extensible wet sticky silk of *L. mariana* contracted immediately into relatively compact masses on its own when web lines were cut. *L. mariana* often made long airborne spanning lines, and was much more likely to move far from the previous website than was *P. vicina*. When on lines near the wire hoop, spiders sometimes bounced up and down as they moved, a behavior not seen in other situations or in the other species. Possibly this movement serves to test the rigidity of the substrate.

II. Frame and radius construction: Eventually the spider's activities became concentrated around a central point where three or more lines intersected (the web's future hub) and the spider repeatedly moved toward the edge and then returned to this point. Some radii were partially replaced, and new radii as well as frame lines were laid. Partial radius replacement was like that of *P. vicina*, and new radius construction was as described by Eberhard 1982 (character F1). Frame construction varied (types A-D in figs. 10-13), but never included breaking the new frame and shifting the attachment outward as in *P. vicina* (e.g., Fig. 4C). Instead, the spider usually made a dragline attachment to the new frame, and then a second attachment to the frame just on the far side of the new radius as it swung its abdomen in this direction prior to returning to the hub (Fig. 14) (a similar slight separation of the second attachment in the same direction occurs in *Metazygia* sp., *Micrathena* sp., and *Eriophora* sp.—Eberhard unpub.). The older frame segment (dotted lines between attachment points [large dots] in Fig. 14) often sagged perceptibly when the spider broke the radius and returned to the hub. Occasionally a spider reinforced or perhaps tightened a frame line by adding a line attached on either side of the new radius before returning to the hub.

Spiders never modified three or more adjacent radii in orderly sequences, nor were frames ever built in strict order in adjacent sectors as in *P. vicina*. Usually it was not possible to observe if the spider made more than a single attachment at the hub after laying a radius, but recognizable hub spiral was almost never laid until radii were complete. One otherwise apparently normal spider seemed to have difficulty in making attachments, and paused perceptibly each time it attached; this spider made only a single attachment as it arrived at the hub after laying most radii; occasionally it made up to three attachments prior to leaving to build the next radius.

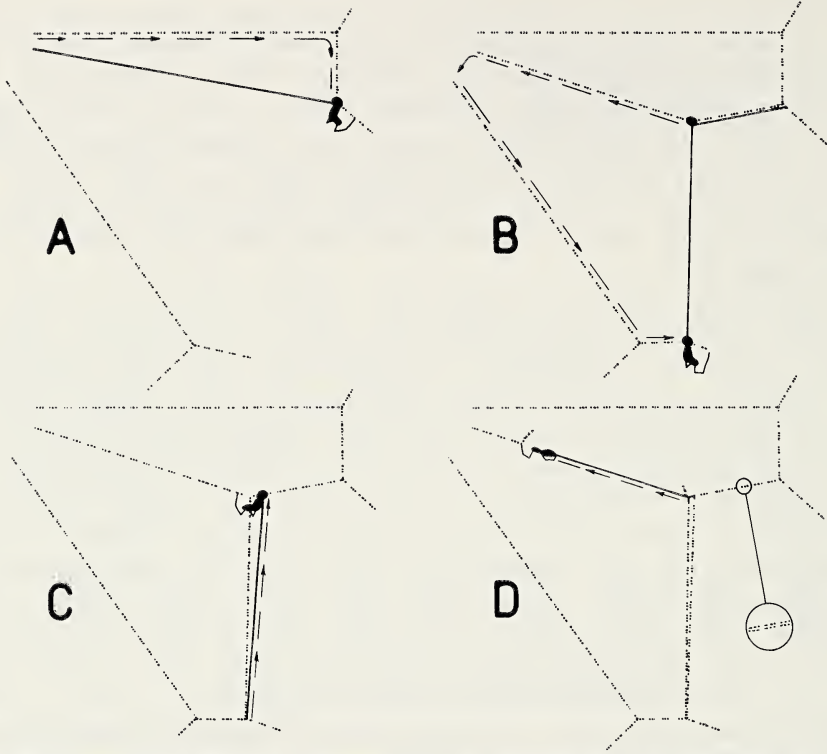


Figure 10.—Sequence of events in *L. mariana* frame construction Type A (conventions as in Figs. 3 and 4).

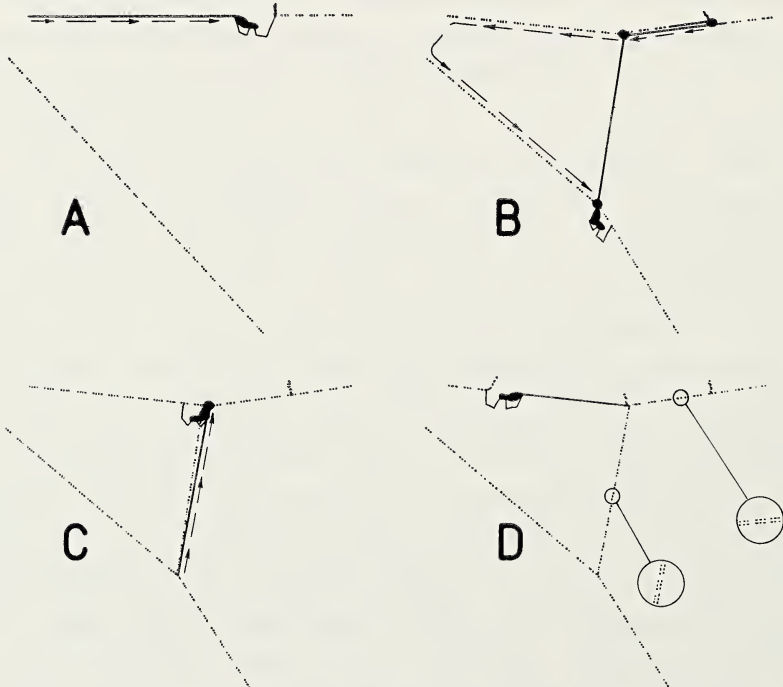


Figure 11.—Sequence of events in *L. mariana* frame construction Type B (conventions as in Figs. 3 and 4).

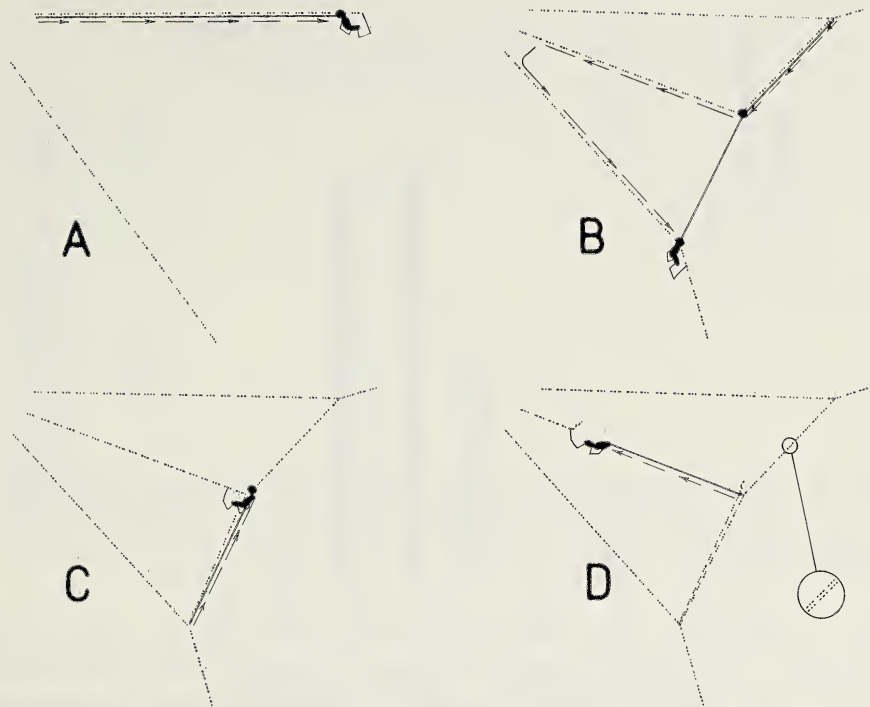


Figure 12.—Sequence of events in *L. mariana* frame construction Type C (conventions as in Figs. 3 and 4).

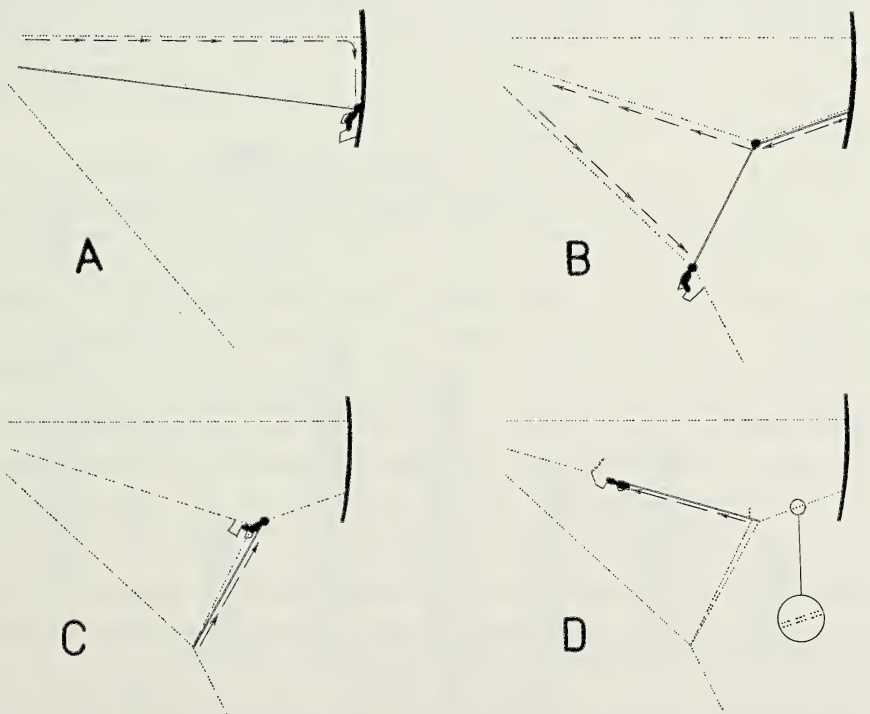


Figure 13.—Sequence of events in *L. mariana* frame construction Type D (conventions as in Figs. 3 and 4).

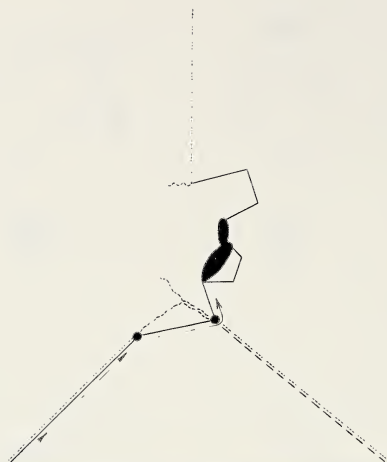


Figure 14.—Details of last attachment in frame construction sequences of *L. mariana* (e.g., D in Figs. 12, 13). As the spider breaks the radius (vertical line) it attaches to the frame on both sides of the original radius-frame attachment, thus allowing a short segment of the frame to go slack (conventions as in Fig. 3).

Frame construction was intercalated with other activities such as radius construction, and showed a similar distribution throughout web construction to that in *P. vicina* (Fig. 9). Partial replacements of radial lines had the same general pattern (Fig. 15), but had a stronger tendency to occur later in construction ($P < 0.05$) comparing webs $>30\%$ finished with earlier stages of construction in the two species). Frames were less likely to be built in succession by *L. mariana* than by *P. vicina*: the behavior immediately preceding frame construction was more often radius construction, and less often frame construction in *L. mariana* ($P < 0.01$ for both, $N = 84$ for *L. mariana*, 68 for *P. vicina*). The most common major type of frame construction (Figs. 10-13) was A (60% of 93 in study webs), followed by C (19%), B (15%), and D (5%).

In contrast to *P. vicina*, the choice of exit radius was not consistent. In only 100 of 211 cases was the side chosen the same as that for the previous radius ($P > 0.5$). The angles between the last six radii were also larger in *L. mariana* (Fig. 16, $P < 0.01$). This was due to the tendency of *L. mariana* to lay successive radii in opposite halves of the web rather than to there being fewer radii in *L. mariana* webs; finished *L. mariana* webs averaged 21.4 ± 3.2 radii while those of *P. vicina* averaged 18.3 ± 4.1 . Nearly 60% of the radii in *L. mariana* webs made angles of more than 120° with the radii that immediately preceded them.

***Nephila clavipes*.**—Mesh on either side of the orb was built prior to and during the first stages of orb construction. No behavior resembling PHR was observed. The mesh was also frequently extended after part of the sticky spiral was complete. Mesh construction was very complex, but included some components of radius and frame construction. It will not be described here.

I. Exploration: Exploration behavior included descents on single vertical lines, occasional long periods of immobility, and "around the corner" substrate attachments. On four occasions a spider went all the way (360°) around a wire or a string in making such an attachment. A central area (the future hub) where lines converged was always established very early in construction, both in webs built from scratch and those with a mesh already present. Commonly the spider

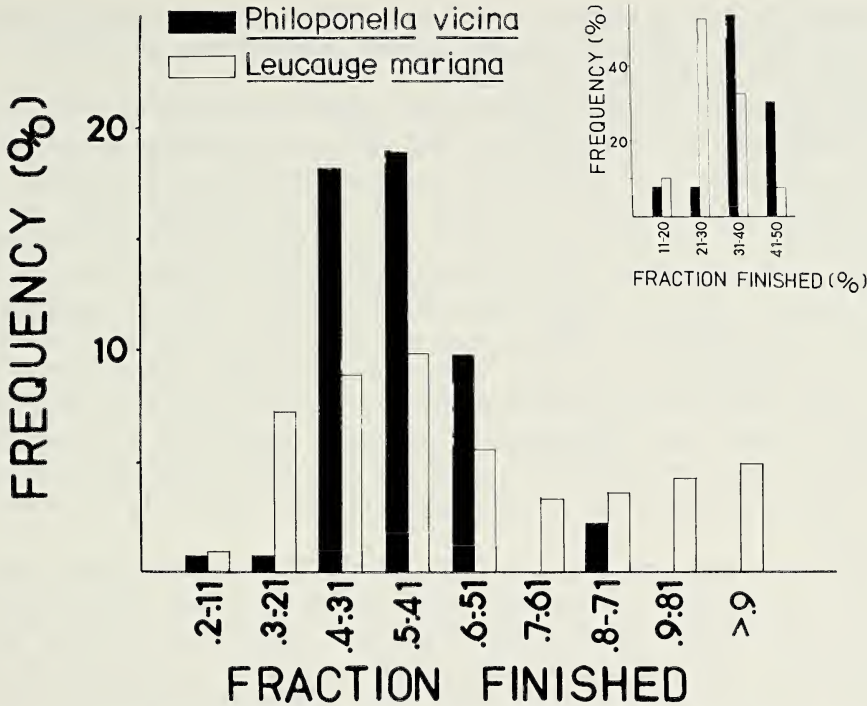


Figure 15.—Relative numbers of partial replacements at different stages of orb construction by *P. vicina* ($N = 72$ replacements in 17 webs) and *L. mariana* ($N = 154$ replacements in 40 orbs) (state of construction indicated by fraction of final number of radii already built). Since some observations began after the first radii had been laid, replacements made in the very earliest stages (<0.20) are under-represented (inset shows the percentage of the final number of radii already present when observations began).

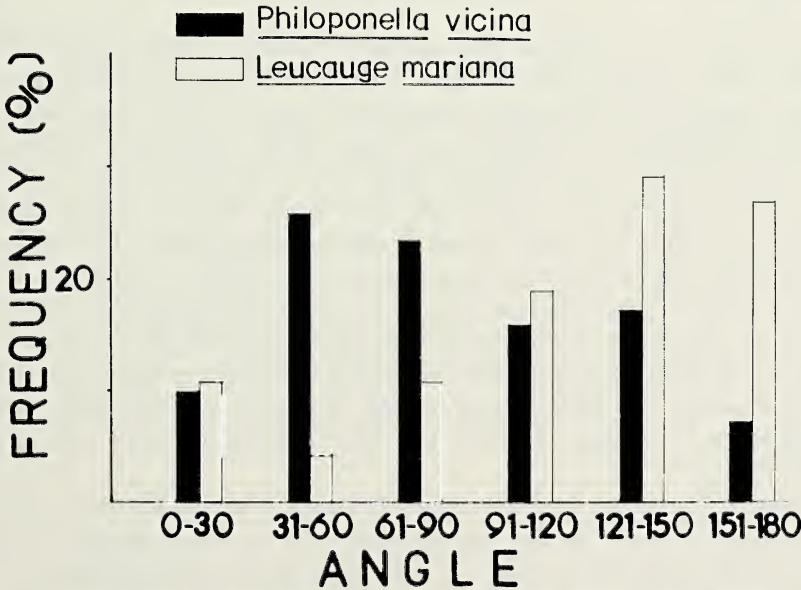


Figure 16.—Distributions of angles between successive radii for the last five radii laid in 16 *P. vicina* and 18 *L. mariana* webs (partial replacements are not included).

expanded the web by walking to the edge and then moving sideways along the substrate before attaching its dragline. Spiders usually slowed appreciably as they moved from a silk line onto the substrate.

Although spiders usually returned from excursions away from the hub along the dragline they had laid on the way out, they never performed one of the most common behaviors of *P. vicina* and *L. mariana*: move away from the hub, attach the dragline, then turn back and break and replace the dragline just laid while moving back to the hub (e.g., Fig. 3). Spiders were capable of breaking and reeling the line they were on, but did this only while removing lines which had not just been laid, and nearly always (40 of 42 times) while moving away from the hub. Many other lines were broken and then simply released and allowed to sag free; breaks of this sort often occurred while the spider was at the hub (14 of 43 cases). Since lines were seldom shifted or replaced, the site of the hub did not change as lines were reconnected as sometimes occurred in *P. vicina* and *L. mariana*. In one case, however, a second hub developed during mesh construction and became the hub of the orb while the first "hub" came to be in the mesh on one side.

Some radii were added early in orb construction without breaking lines: the spider moved away from the hub on a pre-existing radius and then sideways along a frame line or the substrate, attaching its dragline and returning along it, reinforcing it with a second dragline. Other excursions of this sort (6 of 14) resulted in two new radial lines, as the spider continued sideways after the first attachment and attached its dragline a second time before returning to the hub along the line laid on the way out. Neither of the other two species exhibited these behaviors.

II. Frame and radius construction: Frames were never laid in strict order as in *P. vicina*. Hub loop construction did not begin until several radii, a substantial amount of mesh, and often some of the frames had been laid. Once it commenced, hub loop construction occurred after each excursion to build radii or frames.

Frame construction behavior was extremely variable. Types A and B (Figs. 17, 18) were most common (frequencies were 39 and 12% respectively in 101 sequences observed). Twenty-eight additional types of frame construction were seen, none repeated more than three times. Some alternative behaviors were closely related to the most common types. For example one (Fig. 19) was the same as B except for an extra trip across the sector. The points where attachments were made in both A and B varied substantially. Thus the variant in Fig. 20 involved the attachment of a second new radius to the end of the first, and that in Fig. 21 attaching the second new radius beyond the first as the spider moved along the frame; both of these behaviors were similar to Type A. Other variants involved laying similar lines but using alternative paths to lay them (Fig. 22), and breaking and reeling lines instead of simply walking along them (Fig. 23). Still further variants, however, had little relation to more typical patterns (Figs. 24, 25).

All types of frame construction involved laying two radial lines in the process of constructing a single frame, and none involved breaking any of the lines laid while the frame was being made; in both respects *N. clavipes* behavior differed from all types of frame construction seen in *P. vicina* and *L. mariana*.

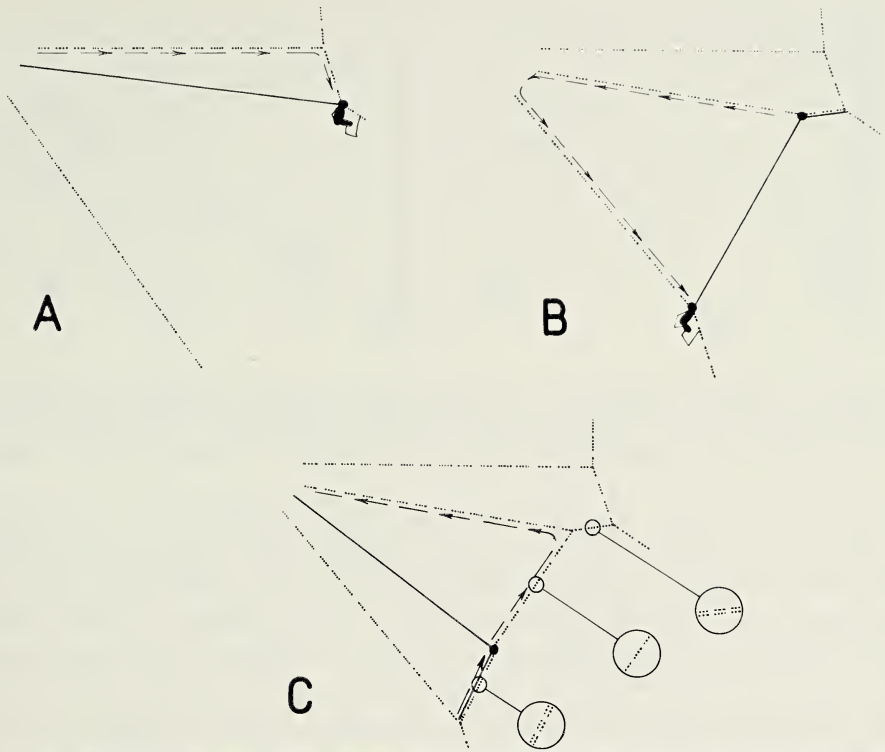


Figure 17.—Sequence of events in *N. clavipes* frame construction Type A (conventions as in Figs. 3 and 4).

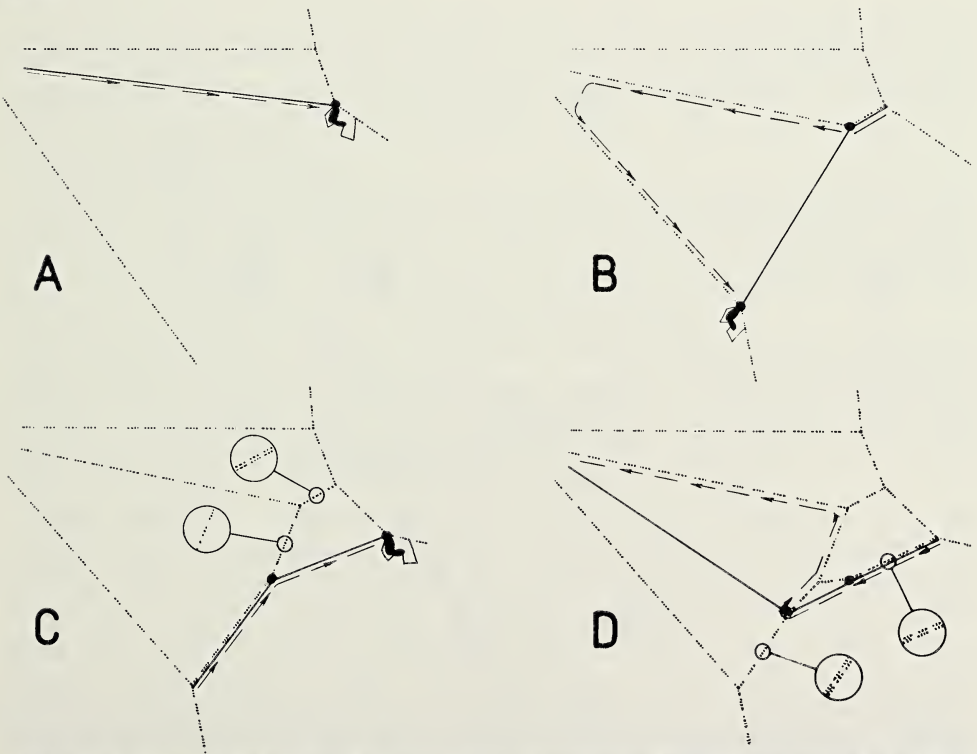


Figure 18.—Sequence of events in *N. clavipes* frame construction Type B (conventions as in Figs. 3 and 4).

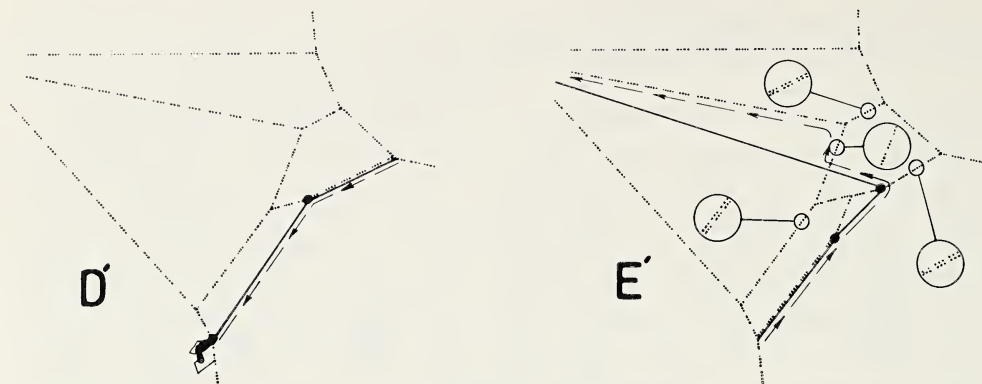


Figure 19.—Sequence of late events in *N. clavipes* frame construction. Behavior was similar to that in Fig. 18 (stages A-C were identical) except the spider made a trip across the entire sector (D') before crossing to lay the second radius and return to the hub (E') (conventions as in Figs. 3 and 4).

Radius construction usually also involved two attachments to the frame and resulted in two radii being laid during each trip away from the hub (Eberhard 1982, character F2). In 44 of 353 cases, however, I was certain that only a single attachment was made at the frame, and the second dragline was laid alongside the first (Eberhard 1982, character F3). Nearly all of these exceptional single radii were relatively short, and 34 of 44 were above rather than below the hub ($P < 0.001$ compared with double radii). The spider always left the hub on the

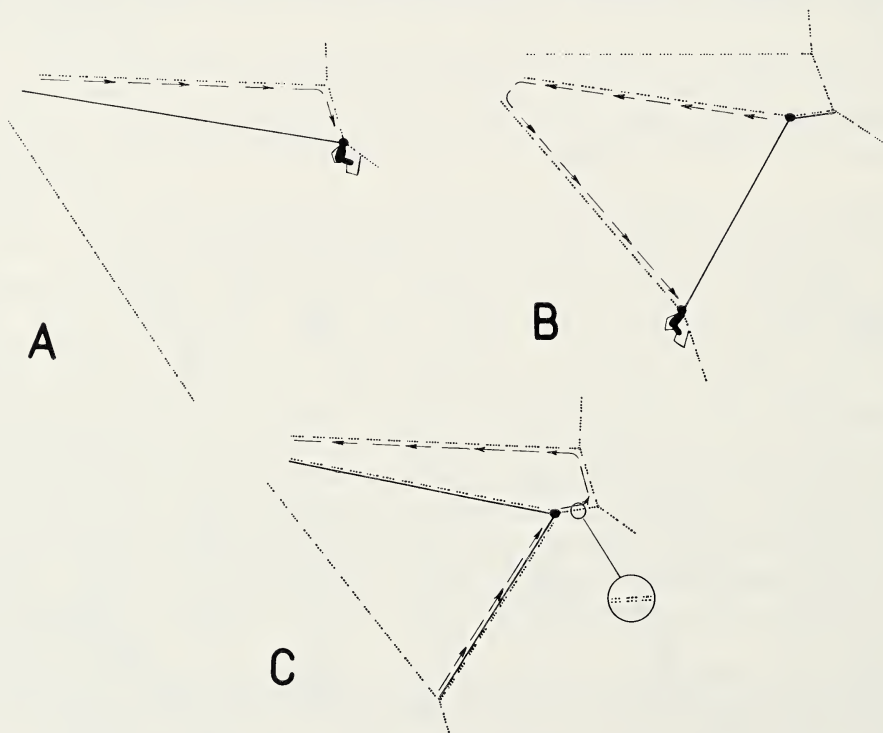


Figure 20.—Sequence of events in *N. clavipes* frame construction similar to that in Fig. 17 except the spider attached the second radius right at the point on the frame where the first was attached (C) (conventions as in Figs. 3 and 4).

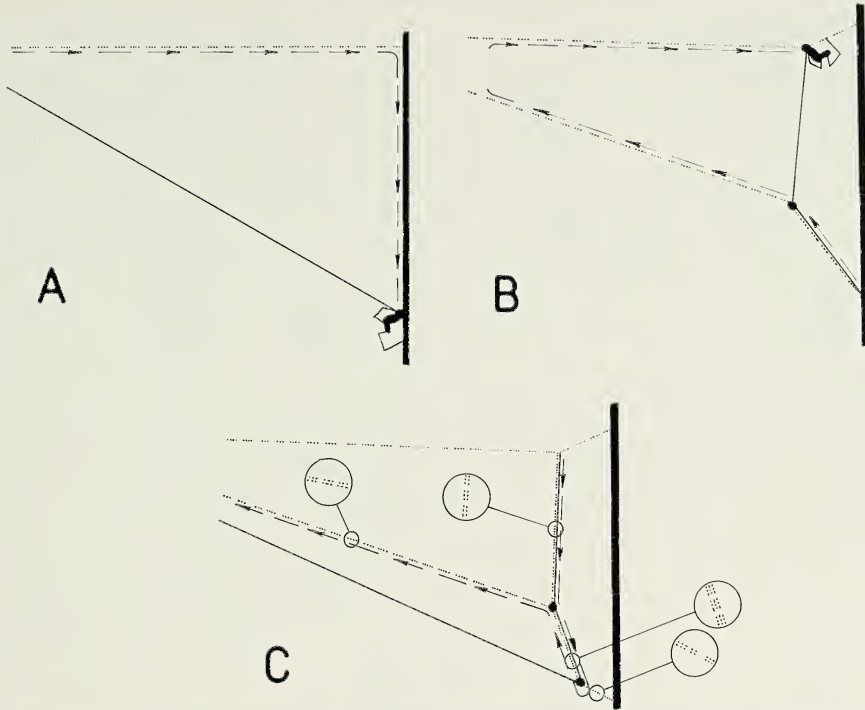


Figure 21.—Sequence of events in *N. clavipes* frame construction similar to that in Fig. 17 except the spider moved along the new frame past the site of the first new radius before attaching the second new radius (C) (conventions as in Figs. 3 and 4).

uppermost of the two radii bounding the sector where the radial lines would be laid ($N > 200$). In four cases a spider interrupted hub loop construction and started away from the hub as if to lay radii, but turned back after moving only a mm or so and resumed hub construction. Similar “false starts” occur in *U. diversus* (Eberhard 1972).

Spiders showed individually consistent differences in the pattern of velocities of movement during radius construction. Some moved inward and outward at more or less the same, relatively slow rate. Others moved part way out relatively slowly, then moved very quickly the rest of the way out, along the frame, and part way in, then slowed again as they approached the hub.

As first described by Hingston (1922) and Wiehle (1931), radius construction continued after the spider widened the space between the loops it was making at the hub, thus changing from hub to temporary spiral construction. Most radii laid during temporary spiral construction were below rather than above the hub (103 of 115 compared with 91 of 238 radii laid earlier, $P < 0.001$).

Other uloborids.—*Hyptiotes cavatus* (Hentz) build triangular webs that probably represent segments of orbs. Previous accounts of construction behavior (Nielsen 1932; Marples and Marples 1937; Eberhard 1982) are not entirely clear on the early stages of construction. I observed only a single web of *H. cavatus* being built, but was able to understand some of what I saw. There was no behavior corresponding to PHR. The single frame was built after two radii were in place, and resembled type B pre-PHR behavior in *P. vicina* in both the replacement of the exit radius and the shift of the frame attachment outward

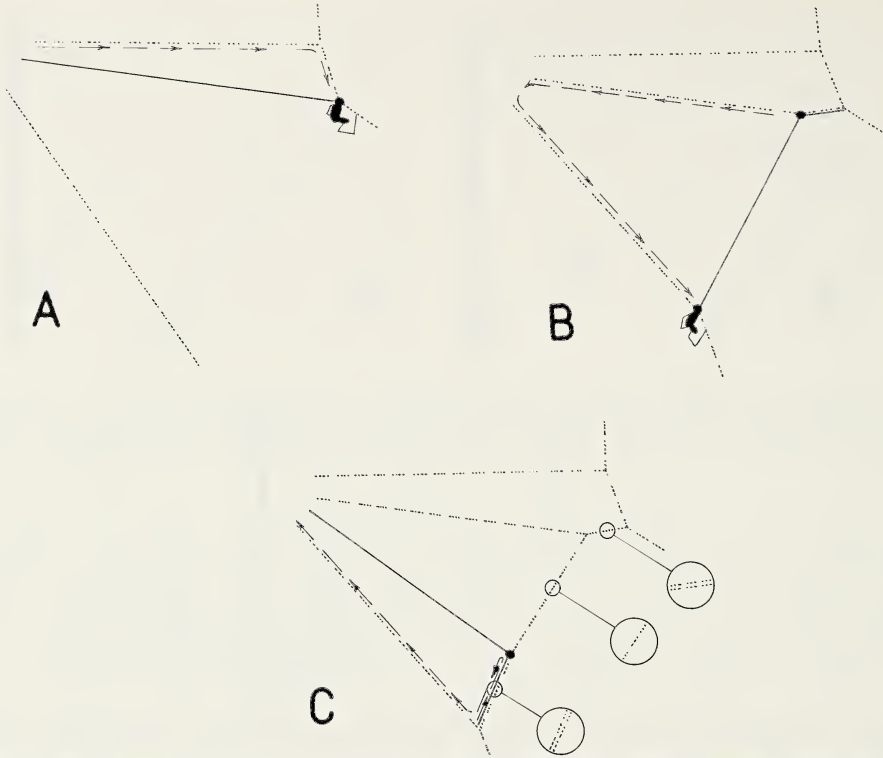


Figure 22.—Sequence of events in *N. clavipes* frame construction similar to that in Fig. 17 except the spider turned back after attaching the second new radius (C), using the second of the two exit radii to make its final return to the hub (conventions as in Figs. 3 and 4).

(Fig. 5). It bore no resemblance to the frame construction behavior reported by Marples and Marples (1937) for *H. paradoxus*. The other two radii were then added without any lines being broken, and without any attachments other than the initial attachments at the hub and the frame. Temporary spiral construction began immediately after the fourth radius was laid, without any hub spiral having been laid. Thus *H. cavatus* radius and frame construction resemble pre-PHR behavior in *P. vincina* except for the last two radii; these resembled post PHR construction except that no hub was made. The descriptions of *H. paradoxus* construction by Marples and Marples (1937) agree on all of these points other than the exception noted above.

Though observations on other genera are still needed, additional observations of construction of single webs by *P. tingena*, *Uloborus trilineatus*, and *Zosis geniculatus* suggest that several of the special behaviors seen in *P. vincina* and *U. diversus* are widespread in uloborids. All species replaced a proto-hub early in radius construction, and broke newly laid frames to shift the frame attachment outward during frame construction (e.g., Fig. 4C). Only after PHR did *U. trilineatus* and *Z. geniculatus* make series of hub attachments during radius construction. Both *P. tingena* and *U. trilineatus* modified a series of radii just before PHR; in *U. trilineatus* I noted that these radii were in strict sequence as in *P. vincina*.

Other araneoid orb-weavers.—Prior to beginning this study, I observed frame construction in 19 tetragnathid and araneid genera (*Nephilengys*, *Tetragnatha*,

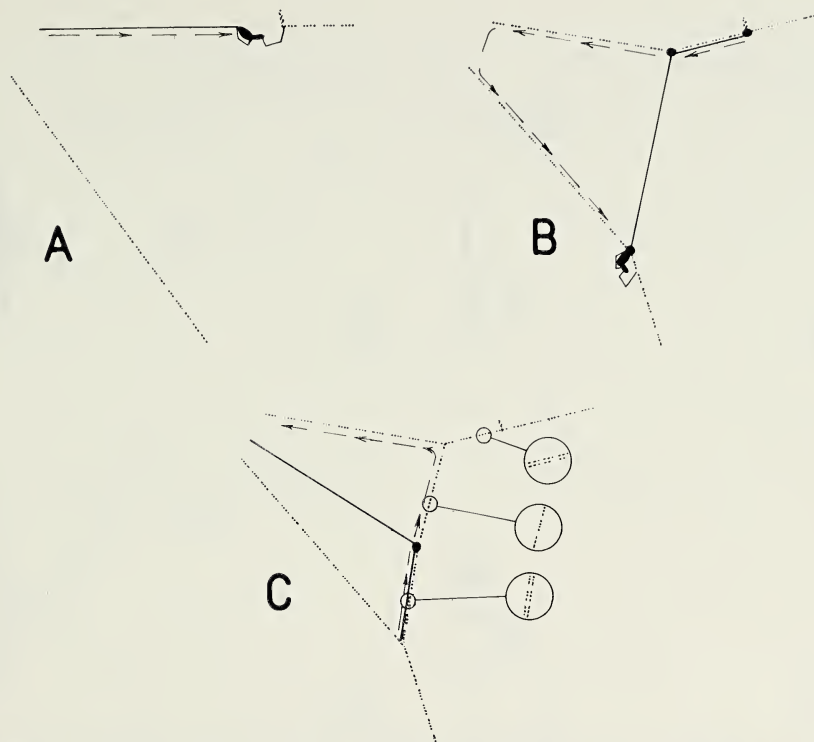


Figure 23.—Sequence of events in *N. clavipes* frame construction similar to that in Fig. 17 except the previous radius on which the spider moved away from the hub was broken and replaced (A) (conventions as in Figs. 3 and 4).

Chrysometa, *Gasteracantha*, *Micrathena*, *Pronous*, *Alpaida*, *Argiope*, *Cyclosa*, *Cyrtognatha*, *Enacrosoma*, *Eriophora*, *Eustala*, *Hypophthalma*, *Larinia*, *Metazygia*, *Parawixia*, *Neoscona*, *Verrucosa*, *Wagneriana*, and *Witica*), in the theridiosomatid *Epeirotypus* sp., and in the mysmenid *Mysmena* sp. While some of my notes do not mention how early in web construction my observations began, very early stages were certainly observed in *Nephilengys*, *Gasteracantha*, *Micrathena* (three species), *Alpaida*, *Cyclosa*, *Hypophthalma*, *Metazygia*, *Neoscona*, *Tetragnatha*, *Epeirotypus*, and *Mysmena*. In no case did any species perform any behavior similar to PHR; since I had observed PHR in *U. diversus* before I made these observations, I am confident that I would have noted anything similar to PHR if it had occurred.

At the conclusion of the study I observed the construction of webs by a different *Metazygia* sp. and *Acacesia hamata*, and again failed to note any behavior remotely similar to PHR.

DISCUSSION

A. Distinguishing characters and their homologies.—In order to compare the behaviors of different groups, it is necessary to first decide which behaviors differ, and which differences or similarities are homologous. Unfortunately, these discriminations are influenced by what seem to be unavoidably subjective decisions. Analysis at a fine level (e.g., movements of given legs) can give



Figure 24.—Sequence of events in complex *N. clavipes* frame construction behavior (conventions as in Figs. 3 and 4).

different results from that at higher levels of organization (e.g., inclusion of the context in which the movement is performed). For instance, I have previously interpreted the tapping behavior of legs I to the side during sticky spiral construction to locate previously laid lines as a possible synapomorphy of Araneidae (Eberhard 1982). But undoubtedly many other orbweavers, and indeed other spiders which do not make orbs occasionally tap their front legs laterally to locate lines (or other objects). So if tapping to the side is itself the unit being compared, the behavior is not a synapomorphy.

The problem of context is acute in behavior since a common and important pattern in behavioral evolution is that of changes in context; a given movement or sequence of movements is transposed from one context to another. This pattern of evolution implies that the standard cladistic techniques of weighting characters equally is inappropriate, since (all other things being equal) convergence via such transpositions is more likely to evolve than is convergence via independent invention or reinvention; transpositions should thus be given less weight in constructing phylogenies.

How great must a change in context be for a homology to be rejected? How can the "size" of a change in context even be measured? These questions seem not to have straight-forward answers. In the example of tapping behavior it seems relatively clear that including the context of the leg movement as a part of the character is reasonable. In other cases, however, this decision is more difficult. Take for example the proto-hub removal behavior of uloborids described in this study. Many araneoid spiders remove the central area of their hubs near the end of orb construction (e.g., Eberhard 1982, 1987c; Coddington 1986a). Is this

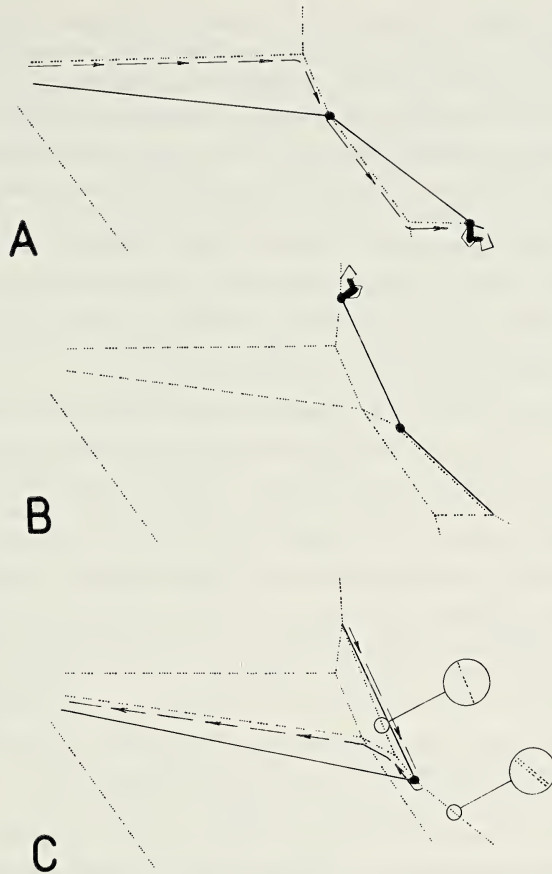


Figure 25.—Sequence of events in complex *N. clavipes* frame construction behavior (conventions as in Figs. 3 and 4).

removal behavior homologous with the PHR of uloborids, but simply displaced to a later position in the sequence of construction? Or is it an independently derived process which has converged on PHR in general form?

Similar problems occur in simple descriptions. Is the behavior in Fig. 11A-B, where *L. mariana* stopped and attached to a line before reaching the substrate different from that in Fig. 13B, where the spider moved past the end of a silk line and laterally (the only direction possible on the wire hoop) before attaching? These problems are related to a general problem plaguing taxonomy—that of deciding how to code characters (behavioral or otherwise), and of the lack of information correlating the amount of phenotypic difference with the degree of improbability that a given phenotype could be derived independently.

As I have no certain answers to these types of questions, the practice adopted in both the descriptions above and the discussion below is conservative: claims of homology are minimized, and differences are thus emphasized. This focus stems both from a reaction against previous oversimplified accounts of construction behavior, and from one of the basic objectives of this study: to provide additional characters to help in the resolution of the controversy surrounding the phylogeny of orb weavers (the final answer to which obviously must depend on as many characters, behavioral and otherwise, as possible). Future workers may decide,

one would hope with better criteria and/or evidence than those which are presently available, that some distinctions made here are unjustified, and combine categories. The opposite process, splitting two categories from a single one in which differences had not been reported, would not be possible.

B. Comparisons between species.—One consistent difference between frame construction by *P. vicina* and that of the araneids *L. mariana* and *N. clavipes* was that all frame lines constructed by the uloborid were broken as the spider returned to the first radius laid, and were then shifted outward along this radius (Figs. 4-8). This behavior never occurred in *L. mariana* or *N. clavipes*. These observations agree with Coddington's (1986a) observations of one genus of uloborid and 17 genera of orb-weaving araneoids, and reinforce his idea that this difference may distinguish uloborids and araneoids.

A second difference was that *P. vicina* usually chose exit radii that were on the leading edges of sectors to be filled during both frame and radius construction, while *L. mariana* showed no preference. The same preference was shown by *U. trilineatus* and by *U. diversus* (at least during frame construction—Eberhard 1972). The difference with *L. mariana* may be partly related to the fact that the uloborids make hub spiral between all or nearly all radii laid after PHR, and are thus turning in an orderly manner at the hub, while *L. mariana* generally makes no hub spiral until all radii are in place. In non-horizontal webs, both *L. mariana* (Eberhard unpub.) and *N. clavipes* generally exit on the upper of the two radii bounding the sector where the radius or frame is to be laid, just as usually occurs in araneids such as *A. diadematus* Cl. (Reed 1968), *Micrathena plana* (Koch), *Verrucosa* sp., and *Cyclosa caroli* (Hentz) (Eberhard unpub.).

The most dramatic differences between the behavior of *P. vicina* and the araneoids are associated with PHR. PHR always occurred in undisturbed *P. vicina*, but never occurred in *L. mariana* or *N. clavipes*. In addition, PHR in *P. vicina* was always preceeded by a strictly ordered sequence of frame construction and radial modifications on adjacent radii, while the order of operations in the early stages of *L. mariana* and *N. clavipes* webs did not follow strict sequences involving adjacent radii. Examination of literature accounts of uloborid and araneoid behavior plus the brief observations of other uloborids and araneoids reported here suggest that both PHR and strict ordering of frames probably distinguish uloborids from araneoids. No araneoid has ever been reported to perform any behavior during the early stages of orb construction that might correspond to PHR (see detailed observations of Hingston 1922; Tilquin 1942; Koenig 1951; Mayer 1952; Witt et al. 1968 as well as the observations reported here). The most similar behavior is the possibly non-homologous hub replacement (see above) performed by some theridiosomatids and anapids after the web is otherwise complete (Eberhard 1982, 1987c; Coddington 1986a). On the other hand, all species of orb weaving uloborids that have been observed (two *Uloborus*, two *Philoponella*, and one *Zosis*) show clear PHR.

The few accounts of sequences of frame lines in araneids (Tilquin 1942 on *Araneus* sp. and *Argiope*; Mayer 1952 on *Araneus diadematus*; Dugdale 1969 on *Micrathena gracilis*), do not show a strict sequence of frames in adjacent sectors of the orb, and Tilquin (1942) states that sequences of frames vary and that radius construction often interrupts frame construction (p. 208 ff.). The only two uloborid orb weavers carefully checked in this study, *U. trilineatus* and *P. vicina*, both modify adjacent radii in strict order immediately preceeding PHR, often

making a series of adjacent frame lines. *U. diversus* also often makes series of adjacent frames (Eberhard 1972). Thus, as far as these incomplete data go, orderliness in frame construction also distinguishes uloborids from araneoids.

Angles between successive radii were larger in *L. mariana* than in *P. vicina* and the same difference apparently occurs when the araneid *M. gracilis* is compared with the uloborid *U. diversus* (Eberhard 1972). Apparently araneids often tend to lay successive radii on nearly opposite sides of the web (Hingston 1920; Witt et al. 1968; Uetz 1986). This difference is probably related to the fact that uloborids lay hub spiral during radius construction while most araneoids lay less or none. Radii on opposite sides may be advantageous in balancing tensions at the hub, but such adjustments would probably not be practical for a spider which is also laying hub spiral, since an excessive number of hub loops would be necessary to allow completion of radius construction, especially in view of the relatively high numbers of radii in some uloborid orbs (Eberhard 1986).

Another possible difference was that *P. vicina* used legs IV to reel in slack silk during frame construction while the others did not. Both *L. mariana* and *N. clavipes* tightened slack frame lines using a different behavior involving the front rather than rear legs. (*L. mariana* was never seen to reel in any line with a leg IV in any context, but *Nephila* sometimes ascends its dragline backwards after attacking prey—Robinson and Robinson 1973). Other uloborids (*Hyptiotes*—Marples and Marples 1937, and Opell 1985; *Miagrammopes*—Lubin et al. 1978) reel in lines with legs IV.

Observations of a slow-moving *L. mariana* as it laid radii revealed that the spider usually failed to lay hub lines between successive radii. Hub lines were also not laid during the early stages of radius construction by *N. clavipes*. These observations are not in accord with Coddington's statement (1986a: 344) that both "araneoids and uloborids construct frames and radii as a subroutine within hub construction." Since it is often very difficult to determine how many hub attachments are made between successive radii (I was generally unable to decide, for example, whether multiple attachments were made by *P. vicina* before PHR), Coddington's claim should be treated with caution.

Changes in the types of radius and frame construction behavior before and after PHR which are similar to those of *P. vicina* appear to occur in *U. trilineatus*, *Z. geniculatus*, and *P. tingena*. Similar changes in frame (but not radius) construction occurred as web construction in *L. mariana* progressed. In all cases there was a gradual reduction in the removal of lines already in place in the web.

The order and kinds of lines laid during frame construction behavior was clearly variable in each of the three species studied in detail here. Both *P. vicina* and *L. mariana* had several common patterns, and additional rare variations. Probably a few further variants remain to be described, perhaps including some of the sequences I saw but failed to understand (see Methods). The behavior of *N. clavipes* was much more variable, and the total number of variations may be quite high (>50?). Some literature descriptions of other species' behavior may represent still further variations (see Tilquin 1942 and Reed 1968 on *Araneus*; Marples and Marples 1937 on *Hyptiotes*). This variability contrasts with the stereotypy seen in later stages of orb construction (Tilquin 1942; Eberhard 1982). As has been noted before (Witt et al. 1968; Eberhard 1972), an orb weaver gradually isolates itself from its surroundings and from the need to respond to

them as it builds, and it is perhaps not surprising that building behavior in later stages is more stereotyped.

Some shifts in *P. vicina* behavior before and after PHR are not entirely consistent, and may represent imprecision in its behavior (Eberhard in press). For example, behavior typical of pre-PHR such as short partial replacements occasionally appeared just after PHR (6 of 130 replacements in the study webs). Such mixing was especially pronounced when spiders built after their first radii and frames of the morning had been destroyed.

C. Implications regarding the evolutionary origin(s) of orbs.—Several lines of evidence from this paper suggest that the transitions in building behavior postulated by the monophyletic and polyphyletic theories of the origin of orb webs differ less than has been previously appreciated. Coddington (1986a) noted that the similarity between uloborid and araneoid frame construction behavior argues for a monophyletic origin of orbs, since other “perfectly feasible alternatives” exist and are actually described in mistaken accounts in the literature. I agree that these published accounts are probably mistaken, but not that they are so obviously feasible for spiders. There are two kinds of mistakes. In one (Comstock 1940; Levi and Levi 1968; Levi 1978) the spider is described as establishing a frame line by running along the substrate from one anchor to another. This is probably usually physically impossible in nature, where webs are often attached to objects which are too separated for the spider to walk directly between them (e.g., many leaves, twigs), and this behavior did not occur even in the wire frames of this study. The other type of error (McCook 1889; Hingston 1920; Dugdale 1969) describes the frames as being laid before any radii are built. But from very early in the exploratory phase of both uloborids and araneoids there are intersections between lines at central points within the area where the orb will be built, and the spider’s activities seem organized around these points as it moves out from them toward the edge of the web, then returns (see Tilquin 1942; Koenig 1951; Mayer 1952; LeGuelst 1966; and Eberhard 1972 as well as this study). In fact, this general radial type of pattern of spinning also occurs in other spiders that do not build orbs, and may be very ancient in spiders (Eberhard 1987d). In sum, the possibility that very ancient, pre-orb traits plus “fabricational constraints” (Coddington 1986a) explain the similarity between uloborid and araneoid frame construction rather than more recent common ancestry of the two groups is more likely than suggested by Coddington (1986a).

Two related points deserve mention. Feasible alternatives for radius and frame construction do exist which neither uloborids nor araneoids are known to employ. These involve the spider not retracing the line it has just laid as it returns to the hub (e.g., Fig. 26). Thus the spider’s tendency to turn and retrace its steps hubward along the same radial line it has just laid, in preference to using other nearby lines is a character shared by uloborids and orb-weaving araneoids. Whether this character is primitive or derived with respect to that of possible sister groups is not certain. The fact that *Filistata* returns “hubward” (toward its retreat) along the more or less radial line it has just laid while spinning sticky silk (Eberhard 1987d) suggests this may be a primitive trait.

A second point is that the variation in frame construction behavior documented here makes comparisons between uloborids and araneoids more difficult to interpret. For instance, Coddington (1986a) notes that araneoid and uloborid frame construction behavior is “strikingly similar”, noting with reference

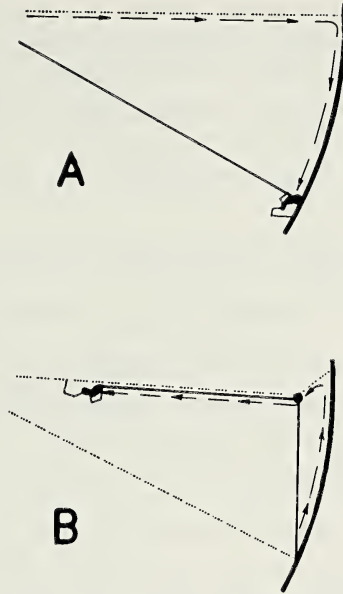


Figure 26.—A simple, feasible frame construction sequence which is apparently never used by orb weavers, in which the spider fails to return to the hub along a newly laid radial line (B).

to *U. diversus* and *A. diadematus* that “both construct a radius each time they construct a frame line.” As shown here, this statement is incorrect for both *P. vicina* (Fig. 5) and *L. mariana* (Fig. 11). Some variants of frame construction are similar in the two species (Figs. 4 and 10, 5, and 11, 8 and 12), while others may be unique to one or the other (Figs. 6, 7, 13). It is difficult to decide how great the degree of difference between two behaviors should be to merit recognizing them as being different (see discussion above).

The behavior of *N. clavipes* is probably primitive with respect to that of *P. vicina* and *L. mariana* in at least two respects. The great variability in frame construction is probably primitive, since it seems likely that the evolution of orb construction involved a rigidification, or weeding out of much greater variability in ordering and locations of lines seen in non-orb weavers (Szlep 1965; Robinson and Lubin 1979) (see Eberhard in press). In addition, *N. clavipes* did not break and reel lines during the stages of construction in which deinopids (Coddington 1986b), and uloborids and araneoids do so (this study). This lack of breaking and reeling behavior (which appears to be absent in *Nephilengys* also—unpub.) may also be primitive, since secondary loss would probably be disadvantageous. Breaking and reeling allows the spider to adjust tensions in the web as it is built (Eberhard 1981), to shift the site of the hub as exploration progresses, to eliminate stray lines laid early in the process that are not appropriate for the final web, and to quickly recycle the material from unwanted lines (Peakall 1971; Tillinghast and Townley in press). These functional considerations imply that shifting and replacing lines would be especially important early in orb construction, an interpretation which is supported by the fact that this is when uloborids perform these behaviors.

In addition, the few descriptions of the building behavior of possible outgroups such as theridiids (Szlep 1965; Eberhard unpub. on *Chrosiothes* sp.), pholcids

(Eberhard and Briceño 1985; Briceño 1985) and a diguetid (Eberhard unpub. on *Diguetia canities*) do not include breaking and reeling, suggesting that breaking and reeling may be a derived behavior. The theridiid *Synotaxus* does break and replace dry lines, but the behavior occurs while the spider is producing sticky lines (Eberhard 1977), and may not be homologous with breaking and reeling during frame construction. Clearly, additional data from possible sister groups are badly needed.

If *Nephila*'s highly variable construction behavior and its lack of breaking and reeling in radius and frame construction are both primitive, then the circumstances under which the argument for a monophyletic origin of orbs can be true are limited in such a way that differences between the character state transitions in the mono- and polyphyletic hypotheses are reduced. This conclusion is based on the following considerations. *Nephila* shows several synapomorphies with other orb weaving araneoids (aggregate glands, flagelliform glands, serrate hairs, paracymbium on male palp, inner leg IV pushes sticky silk when attach—Coddington 1986a), and so is likely to be more closely related to these spiders than to uloborids or deinopids. The argument that all orb weavers are descended from a single cribellate orb-weaving ancestor thus has two possible forms with respect to breaking and reeling: either the common ancestor used breaking and reeling behavior and *Nephila* has secondarily lost this ability; or the ancestor lacked this character, and it was acquired independently in both uloborids and other araneoids. Similarly, either the ancestor lacked relatively invariable frame construction, or *Nephila* secondarily lost it.

Since secondary loss is unlikely on functional grounds, at least in the case of breaking and reeling (above), the more likely monophyletic account is that the ancestor lacked this behavior. This in turn would imply that if orbs are monophyletic, breaking and reeling was acquired independently by both uloborids and non-nephiline araneoids. In each line the behavior would then have revolutionized orb construction, being incorporated into exploration, radius and frame construction, and perhaps in hub removal in somewhat different ways.

This evolutionary sequence is relatively similar to the alternative, polyphyletic hypothesis in having major parts of orb construction evolving convergently. In sum, the observations here imply that even if all orb weavers are descended from an orb-weaving ancestor (more data are needed on this point—Shear 1986), some major aspects of orb construction behavior appear to have arisen independently in different evolutionary lines.

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RESEARCH NOTES

**DISCOVERY OF *CAVIPHANTES SAXETORUM*
IN NORTH AMERICA; STATUS OF
SCIRONIS TARSALIS (ARANEIDA, LINYPHIIDAE)**

The genus *Caviphantes* Oi, 1960 was reviewed by Wunderlich (1979), who placed in synonymy the somewhat better-known name *Lessertiella* Dumitrescu and Miller, 1962; that synonymy is now generally accepted. The genus contains four species: *Caviphantes samensis* Oi from Japan, *Caviphantes dobrogicus* (Dumitrescu and Miller) from Rumania and southwestern U.S.S.R., *Caviphantes pseudosaxetorum* Wunderlich from Nepal, and *Caviphantes saxetorum* (Hull) from Britain and Germany. The first two occur in caves, soil, and litter; the third in litter; the fourth under stones in dry beds and sandy banks of rivers.

In Europe, *C. saxetorum* is rare as well as habitat-limited (Cooke and Merrett 1967; Roberts 1987); its discovery in Oregon, U.S.A., is therefore remarkable. The specimen, a male at the Thomas Burke Memorial Washington State Museum, University of Washington (UWBM), does not differ significantly from the best available description (Cooke and Merrett 1967). I am forced, therefore, to consider it a member of this species despite the geographic separation. The collection data are as follows:

OREGON: Lane Co.: Lookout Creek (564 m), 44.223°N 122.228°W, 13 April-4 May 1983 (pitfalls), G. Parsons leg. The site is in the H. J. Andrews Experimental Forest. The macrohabitat is a seral forest of 40-year-old *Tsuga heterophylla* (western hemlock), with understory of ferns, *Polystichum munitum*, and the herb *Oxalis oregona*. Due to its collection by pitfall, the microhabitat of the specimen is unknown; the site is 375 m from the boulder-strewn bed of Lookout Creek but only a short distance from an intermittent tributary, so the habitat may be the same as in Britain.

I think it highly unlikely that this collection represents an introduced population. In Europe the species is far from synanthropic, and the Oregon locality is remote (11.5 km from the nearest small town; 70+ km from Eugene, the nearest commercial center). If *C. saxetorum* is, as I suspect, a truly Holarctic species, it would be expected, and should be searched for, in other North American and Eurasian localities.

The tracheal system of *Caviphantes* is linyphiine, not erigonine (Millidge 1984). Millidge placed the genus in his "*Stemonyphantes* group," an informal assemblage of linyphiine spiders with "primitive" (i.e., simple) female genitalia. I feel that *Caviphantes* and its near relatives fit fairly well in Millidge's formal subfamily Linyphiinae, having in common an epigynal atrium formed between the dorsal and ventral plates which contains the genital openings (see Millidge 1984: fig. 17). The only difference from "typical" Linyphiinae is that the dorsal plate is not extended in a scape. *Caviphantes* shares major genitalic features, the

epigynum as described above and complex palp with long, looped embolus originating centrally, with its nearest relatives, the European *Mioxena* and the American *Scironis* (for details of palpal conformation see Millidge 1977; Cooke and Merrett 1967). *Mioxena* has the simplest palp of the three, *Caviphantes* the most complex. These three genera have identical chaetotaxy: tibial spines 2-2-1-1, TmI = 0.3-0.45, TmIV absent.

The genus *Scironis* Bishop and Crosby, 1938 has hitherto been considered erigonine. I have done a tracheal determination on a male *Scironis tarsalis* (Emerton) from Alaska (UWBM) and found a linyphiine-type tracheal system (Millidge 1984: fig. 130). The epigynum (females, UWBM, from Washington and Alaska) is very similar to that of *C. saxetorum*, but the palp (Bishop and Crosby 1938: fig. 35) is sufficiently distinct to maintain *Scironis* as a genus, which as far as known is monotypic. *Scironis autor* Chamberlin has been transferred to *Scotinotylus*, and *Scironis sima* Chamberlin also belongs elsewhere. The *Scironis* palpal conformation superficially resembles that of the erigonine *Pocadicnemis*, but the tracheal systems preclude close relationship.

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ENTOMOPHAGOUS FUNGI AS MORTALITY AGENTS OF BALLOONING SPIDERLINGS

Organisms with high fecundity are expected to have a high incidence of juvenile mortality. Many species of spiders produce a hundred or more eggs per egg sac and multiple broods per year. Juvenile spiders are subject to the usual array of parasites and predators, but then those spiderlings that balloon for dispersal are confronted with many additional mortality factors. Those that have been cited in the literature are predation, landing in an inhospitable site, and harsh weather conditions.

I propose that an additional and significant mortality factor affecting ballooning spiders is infection by entomophagous fungi. Several investigators have reported on adult spider mortality by fungi in the field and in the laboratory. In Panama, *Nomuraea* sp. was found on five species of the Araneidae (Nentwig 1985). Humber and Rombach (1987) found the fungus *Torrubiella ratticaudata* its anamorph *Gibellula clavulifera* var *alba*, as well as *G. pulchra* and *Nomuraea atypicola* on salticid spiders. In a recent laboratory study, Greenstone et al. (1987) demonstrated that spiders across a broad taxonomic range are susceptible to the fungus, *N. atypicola*. Here I present evidence of fungal attacks on juvenile spiders found in a southern deciduous forest.

I collected ballooning spiders from a 45 m forest-meteorology tower in Oak Ridge, TN from Sept-Oct, 1987 and May-June, 1988. Spiders were collected on traps made of polyvinyl chloride sewage pipe (outside diameter—15 cm, length—94 cm) coated with a fruit tree banding compound (Pest Glue, R. Seabright Industries). I removed spiders with forceps from the traps daily, soaked the spiders in paint thinner to remove the sticky material, and then preserved the spiders in 70% ethanol. I identified the spiders to family with the aid of a Wild dissecting microscope and noted the presence or absence of fungi. Similarly, insects collected on the traps were also examined for the presence of fungi; however no fungal growths were ever seen on insects. Traps were cleaned weekly to ensure that fungi did not grow on the traps, and daily collections of spiders ensured that infection of individuals occurred prior to entrapment.

In the fall study, 98% ($n = 617$) of all trapped spiders were immatures that ranged in size from 1-3 mm. Of these, 20% were infected with fungi that appeared as a round mass of hyphae between leg #1 and leg #2 at the juncture of the coxa and the cephalothorax. All of the infected spiders were immature Thomisidae. Fewer infected spiderlings were observed in the spring (5% of total sample, $n = 318$); however, individuals that represented the families Araneidae, Linyphiidae, Salticidae, Erigonidae, and Thomisidae were infected with fungi. Samples of infected spiderlings were sent to Richard Humber, Boyce Thompson Institute, for identification. Due to the absence of sporulative structures, he was unable to positively identify the fungus; however, based on growth patterns he felt that this fungus was probably a species of *Gibbellula* or *Torrubiella*, some of the most common and widely distributed spider pathogens.

It would be interesting to know if spiderlings are exposed to fungal spores in the egg case, as spiderlings before dispersing, or in air as they are ballooning.

This could easily be tested by collecting and culturing spiderlings at various stages utilizing the techniques described by Greenstone et al. (1987).

The observations reported here imply that pathogenic fungi may be important sources of mortality among spiderlings. Furthermore, infected ballooning spiderlings may play a role in dispersal of pathogenic fungi.

I would like to thank R. Humber for examining the infected specimens, W. Herndon for use of his microscope, and S. Riechert, M. Greenstone, and D. Jennings for comments on the text.

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THE EFFECT OF *HYPTIOTES CAVATUS* (ULOBORIDAE) WEB-MANIPULATION ON THE DIMENSIONS AND STICKINESS OF CRIBELLAR SILK PUFFS

After constructing their vertical triangle-webs, *Hyptiotes cavatus* (Hentz) tense them by reeling in monitoring line thread and holding it between their second and third legs. When a prey strikes its web, a spider releases this slack silk, suddenly reducing web tension and causing the web to shake (Lubin 1986; Opell 1982). This behavior may also change the properties of the web's cribellar capture threads that extend across its four diverging "radii." Like the cribellar threads of other uloborids, those of *H. cavatus* are composed of torus shaped puffs of fine cribellar fibrils deposited around supporting axial fibers (Fig. 1; Opell 1989a). The reduction of web tension that occurs when spiders respond to prey may increase the width of these cribellar puffs, thereby exposing more surface area per unit length of cribellar thread and increasing its ability to hold prey. To determine if this occurs, we measured the properties of taut and slack cribellar threads of *H. cavatus*.

Sixteen adult females were housed individually in frames. From the first web each spider constructed, we collected a taut cribellar thread sample on a microscope slide with five raised adhesive supports spaces at 4 mm intervals (Opell 1989b). From the second web it spun, we collected a slack silk sample by prodding the spider with a brush and pressing the microscope slide against the web the instant the spider released its slack silk.

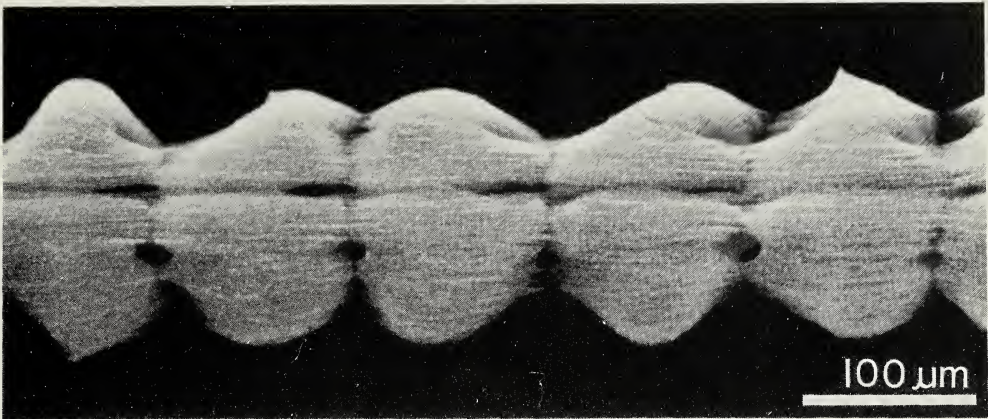


Figure 1.—Scanning electron micrograph of cribellar silk spun by an adult female *Hyptiotes cavatus*.

In two of the 32 web samples taken the cribellar silk puff dimensions of only three of a sampler's four sectors could be measured. In five of the samples the stickiness of cribellar silk in only three of the four sectors could be measured. We measured the width (perpendicular to the thread's long axis) of one puff and the length of a series of ten puffs of the cribellar thread in each sector of a sampler at 125X under a compound microscope equipped with Nomarski optics. The mean values of a thread's dimensions were used for comparisons. Using techniques described by Opell (1989b), we measured the force required to pull a 2.30 mm wide aluminum contact plate free from the cribellar thread in each sector of a sampler. Before each measurement was taken, this plate was gently rubbed with a tissue wetted with acetone and was initially pressed against the thread in each thread sector with a force of 3.03×10^{-5} Newtons. The mean value of a sample's sectors, expressed as the force per mm of contact required to pull the plate free of the cribellar thread, is used for comparisons.

Table 1 summarizes the results of this study. *T*-tests show no significant difference between the mean puff width, puff length, or stickiness ($P = 0.90, 0.43$, and 0.28 , respectively) of cribellar thread samples taken from taut and slack webs.

Table 1.—Dimensions and stickiness of taut and slack cribellar threads from *Hyptiotes cavatus* webs. In each case, sample size is 16.

Variable	Mean	Range	SD
Puff length μm :			
Taut	78	53-103	17
Slack	83	56-116	17
Puff width μm :			
Taut	190	158-220	16
Slack	189	168-232	18
Stickiness in Newtons $\times 10^{-5}$ per mm width of contact plate:			
Taut	4.30	1.71-9.02	2.09
Slack	3.58	1.00-6.65	1.54

This study shows that changes in *H. cavatus* web tension resulting from web manipulation during prey capture do not serve to alter the measured physical or functional properties of the web's cribellar threads. The failure of a spider's behavior to change the dimensions of cribellar thread puffs may occur either because the tensing force exerted on the web's radial elements is too acute to the cribellar threads to initially deform them or because the axial fibers of the cribellar threads resist this elongating force.

However, web-manipulation may yet increase a web's ability to retain prey. Unlike the aluminum plate used in this study, the surfaces of insects are beset with setae that can penetrate the fibril cloud of cribellar threads. By comparing the stickiness of cribellar threads before and after their tensions were altered, this study does not fully evaluate the effect of web-manipulation on a thread's ability to retain prey that remain in contact with it during these changes. By shaking a web and altering its tension, web-manipulation may enhance prey retention by permitting the cribellar thread's looped surface fibrils to better entwine a prey's setae, by causing a struggling prey to contact more cribellar threads, or by more forcefully pressing cribellar thread against the surface of a prey.

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RESPONSES BY SCORPIONS TO FIRE-INITIATED SUCCESSION IN ARID AUSTRALIAN SPINIFEX GRASSLANDS

Scorpions are successful inhabitants of arid and semi-arid grasslands, where they may reach densities of 5000/ha and biomasses of 5-20 kg/ha (Polis et al. 1986). Such grasslands are usually burnt frequently, either by lightning-initiated fires or by Aboriginal people, and yet the responses of scorpions to fire and the subsequent changes in vegetation are unknown. Indeed, in their review of the responses of grassland arthropods to burning, Warren et al. (1987) did not cite any studies of scorpions. In this note, we examine the relative abundance of scorpions in different vegetation states following fire in spinifex grasslands of arid central Australia.

Work was conducted at eight sites in the Tanami Desert, Northern Territory, within 50 km of The Granites (20 32' S, 130 24'E) and 500 km northwest of Alice Springs. Three samples were taken: from 4 April to 2 May 1985; from 18 October to 14 November 1985; and 25 March to 22 April 1986. There was little rainfall during this period, and vegetation declined slightly in cover. Each site was on flat sandplain dominated by feathertop spinifex, *Plectrachne schinzii*, but vegetation varied markedly because of successional change following fire. Two sites each were in areas burnt in the summers of 1983-84 (state 1, burnt about one year prior to the beginning of the study), 1982-83 (state 2), 1979-80 (state 5), and 1976-77 (state 8). Cover of spinifex measured by wheel-pointing (see Griffin 1989a) averaged 6%, 15%, 37% and 39% in states 1, 2, 5, and 8 respectively during the three sampling periods discussed in this paper. Cover of other forbs and grasses averaged 10%, 8%, 1%, and 1% at those times; the principal species were *Leptosema chambersii*, *Scaevola parvifolia*, *Rulingia loxophylla*, *Eragrostis setifolia*, and *Aristida holathera*. Mean cover of shrubs increased from 1% to 8% from states 1 to 8; the dominant shrub species was *Acacia coriacea*. The vegetational changes caused by fire on these sites (i.e., a flush of forbs and grasses followed by regeneration of the spinifex and shrubs) were very similar to those described for *P. schinzii* from a broader region by Griffin (1989b). In this part of the arid zone, *P. schinzii* dominates the ground layer within about five years of a fire and is usually burnt again within 10 years.

Scorpions were captured in pit-traps set for small vertebrate animals. Traps were opened at only one site at any one time, but the order in which the sites were visited was varied in each sample to minimize the chances of systematic error due to changing temperatures over the month-long sampling periods. The traps operated for three days and were set 5 m apart in groups of 10. In the first sample, three groups of pit-traps were spaced about 200 m apart along a transect, but four groups were employed in the second and third samples; thus, the number of pit-trap days was 90 in the first sample but 120 in the other two. A mixture of plastic buckets 15 cm and 29 cm in diameter was used; details are given by Morton et al. (1988). Scorpions were removed from the traps each morning and then preserved in alcohol.

Five species of scorpions were present, but four — *Lychas variatus* (Thorell) and *Isometroides vesus* (Karsch) (Buthidae), and *Urodacus armatus* Pocock and

Table 1.—Numbers of *Lychas alexandrinus* captured in pit traps, and sex ratios of adults, in four different successional states following fire. State 1 was burnt in 1983/84 (1 year since fire), state 2 in 1982/83 (2 years), state 5 in 1979/80 (5 years), and state 8 in 1976/77 (8 years). There were two replicates for each state. Thirty traps were used at each site for the first sample, but 40 for the final two samples; in sample 1, numbers in brackets show the scaled-up data used in subsequent analysis of variance.

	Vegetation state			
	1	2	5	8
Numbers				
Sample 1	12(15)	26(35)	23(31)	13(17)
Sample 2	40	64	39	26
Sample 3	6	58	30	19
Total	58	148	92	58
Sex Ratio (M:F)				
Sample 1	0.75	0.40	0.33	0.29
Sample 2	0.44	0.81	0.67	0.91
Sample 3	0.25	0.23	0.35	0.13
Total	0.45	0.47	0.46	0.41

U. hoplurus Pocock (Scorpionidae)—were seen in small numbers only. Only the buthid *Lychas alexandrinus* Hirst was collected in sufficient numbers to allow statistical analysis (Table 1). *Lychas alexandrinus* is widely distributed in arid and semi-arid Australia. It is a small animal (total length 30 mm) that, in the sandplain environment of the Tanami Desert, shelters in abandoned burrows or nests of other invertebrates. As only three groups of traps were used in the first sample, the numbers of *L. alexandrinus* were scaled up to allow comparison with the later samples. The numbers of individuals were transformed by natural logarithms to normalize variances, and then a two-way analysis of variance was conducted to compare the numbers of *L. alexandrinus* caught in different vegetation states and samples.

The analysis showed that captures of *L. alexandrinus* did not vary significantly with sampling time ($F = 2.585$, $df = 2$ and 12 , $P > 0.2$), but that they did so with vegetation state ($F = 4.825$, $df = 3$ and 12 , $P < 0.05$); there was no significant interaction ($F = 1.085$, $df = 6$ and 12 , $P > 0.5$). Subsequent testing of means with the Welsch step-up procedure failed to identify unambiguously the states which differed, but more individuals were captured in vegetation state 2 than states 1 and 8, with state 5 appearing to be intermediate (Table 1).

In order to look more closely at the difference between states, we examined the condition of each scorpion by dividing the length of its carapace into the cube root of its wet weight (we were able to do this because there was a significant correlation between preserved wet weight and dry weight; $r = 0.93$). In both males and females, these indices of condition varied significantly across the four vegetation states; both sexes showed better condition in state 5 than elsewhere (Table 2). These data add weight to the conclusion that populations reacted significantly to changes in vegetation, and that the middle of the successional gradient supported more active and relatively larger scorpions.

The sex ratio of male to female scorpions fluctuated substantially between samples (Table 1). These discrepancies may be due to different activity patterns between the sexes in relation to breeding, or perhaps in response to short-term weather conditions. Although the mean ratios appeared to be similar across the

Table 2.—Condition of male and female *Lychas alexandrinus* in four vegetation states, as estimated by dividing carapace length into the cube root of wet weight. Means \pm standard deviations are shown, with sample sizes below. Differences among states were examined with Kruskal-Wallis tests. ** $P < 0.01$, *** $P < 0.001$.

Sex	Vegetation state				Chi square
	1	2	5	8	
Male	0.131 \pm 0.006 24	0.129 \pm 0.006 80	0.132 \pm 0.006 53	0.129 \pm 0.005 31	11.805**
Female	0.132 \pm 0.005 9	0.131 \pm 0.006 33	0.137 \pm 0.007 23	0.130 \pm 0.008 13	12.452**
Total	0.132 \pm 0.006 33	0.130 \pm 0.006 113	0.134 \pm 0.007 76	0.130 \pm 0.006 44	21.798***

vegetation states, our results concerning the effects of burning must be interpreted with caution because they may be affected by patterns of foraging and reproductive behaviors.

Although our study does not fully explain all observed changes in capture rates, it does provide evidence that at least one species of grassland scorpion persists readily through fires. Our data indicate that *L. alexandrinus* was active a year after a fire in numbers that were statistically indistinguishable from those in areas of mature spinifex. Increased numbers in traps were observed two to three years after burning, and scorpions were in better condition five years after a fire. We suspect that scorpions generally have the capacity to withstand perturbations such as fire. Most live in burrows, either their own or those of other species, or beneath persistent shelters (Polis 1988). It is worth noting Eastwood's (1978) suggestion that burrowing scorpions in South Africa were abundant after fire, but that non-burrowing species were less likely to persist through frequent fires. Scorpions are able to eat large quantities of food at one time and to store excess energy in the hepato-pancreatic glands. This ability, coupled with their extremely low metabolic rates, allows scorpions to survive without food for many months (Polis 1988). These characteristics, together with their long life-spans, probably allow many scorpions to avoid the direct effects of disturbances such as fire and to take advantage of the subsequent altered conditions.

In summary, our information shows that *L. alexandrinus* is caught more frequently several years after spinifex grasslands are burnt. Populations did not appear to be reduced in numbers a year after fire, and so they seem capable of taking advantage of the habitat changes set in train by burning.

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BOOK REVIEW

Platnick, N. I. 1989. *Advances in Spider Taxonomy 1981-1987: A Supplement to Brignoli's A Catalog of the Araneae Described Between 1940 and 1981* (edited by P. Merrett). Manchester University Press. Distributed exclusively in the United States and Canada by St. Martin's Press, \$190.00.

This magnificent 673-page volume continues the work of cataloging and summarizing the many taxonomic changes that have occurred within the Order Araneae since the classic works of Roewer, Bonnet, and Brignoli. In his introduction Platnick thanks the makers of his word-processing software and computers, and indeed the ease such tools confer on this sort of work can scarcely be overstated. Brignoli wrote his catalog on paper slips, Platnick wrote his on disk. We can look ahead to that day (probably not far off) when such works will be available in database form as well. Given the rather stiff price for this volume and the flexible access that computers allow, that day can not arrive too soon.

The volume is remarkably error free. The author and his able arachnologist editor Peter Merrett deserve high praise for this. I found no errors within the body of the catalog. In fact it corrected a long standing misunderstanding on my part (it's *Daramulunia* Lehtinen, not *Daramuliana*).

The bibliography is, of course, comprehensive (roughly 1200 references); as in the catalogs of Roewer and Brignoli, only taxonomic literature is included. The style follows that of Roewer and Brignoli in that entries are grouped first by year rather than alphabetically by author. I personally find this style less usable, and hope that future volumes will adopt the former style. *Advances in Spider Taxonomy* resumes Roewer's formula for taxonomic entries, which delivers succinct information on illustrations, descriptions, transfers, and synonymies. It is fast and easy to use.

Knowing what to include and what to omit must be a problem for cataloguers. Platnick explains the convoluted history of araneological cataloging in his preface. Cataloging took a severe turn for the worse when Brignoli omitted synonymies and transfers of pre-Roewer names (those published before 1940 or 1954) from his compilation. Given that a huge number of spider names are pre-Roewer, this omission condemned the user to just the sort of memorization of the primary taxonomic literature that one expects catalogs to obviate. I am delighted to report that *Advances in Spider Taxonomy* is back on track, and includes all such synonymies and transfers for the time period covered. It is thus fully comprehensive and complete. The 1940-1981 hiatus due to Brignoli's omission remains, but future volumes will correct this lack.

Platnick does draw his own line, however. He omits fossils, subfamilial and subgeneric groupings, and mentions of taxa in purely faunistic works unless accompanied by useful illustrations. Neither does he list instances where an author provided only general habitus illustrations. These are reasonable pragmatic decisions that will not impede most taxonomic work.

That *Advances in Spider Taxonomy* is indispensable to researchers and especially to taxonomists scarcely needs saying, but it also provides information of a more general nature. The Order Araneae as a whole contains roughly 34,000 described species, grouped in 2944 genera in 105 families (N. I. Platnick, pers. comm.). As such, it falls well within the ten most diverse ordinal groups on earth (whatever an "order" is. . .). At the generic level Salticidae, with 490 genera, reigns supreme. Linyphiidae is second with 386 genera. Even if one excludes monotypic salticid and linyphiid genera, their competitors still are probably less diverse; Thomisidae and Gnaphosidae have 160 and 141 genera, respectively. Fourteen families remain monotypic at the generic level.

Advances in Spider Taxonomy records about 7700 taxonomic entries since 1981, including 230 newly described genera, and roughly 2581 newly described species. (Due to possible counting errors, numbers of species reported hereafter are rounded to the nearest ten.) Taxonomic practice seems to be improving: 1420 species were described from both sexes; 720 from females only; 440 from males only; and just one new species was based on juvenile specimens only (in 1982). Platnick made a special effort to cover the Soviet and Chinese literature, which heretofore has received only spotty coverage in the West. For example, 150 of the new species descriptions pertain to China and 180 to regions within the USSR. As one might anticipate, the region most productive of new species is Latin America and adjacent archipelagoes (690), followed by Africa and her islands (320), Australia (250), North America (210), Japan and Korea (130), and India and Sri Lanka (100). New species still turn up with respectable frequency in Europe and adjacent Mediterranean islands (120), although discoveries in England (that best known region) seem to be petering out at last. About a third of all genera (1089 in 83 families) are found in the Neotropics.

This volume also conveys much about our knowledge of the phylogeny and diversification of spider lineages. Early to mid-20th century phylogenetic work on spiders can be fairly summarized as cautious tinkering with Eugène Simon's impressionistic classification. However, in the late 1960s and early 1970s P. T. Lehtinen and R. R. Forster showed that the old Cribellatae (which Simon accepted) was nothing less than fictitious. This insight burst like a bomb among araneologists, effectively shattered the complacency based on the traditional classification, and rendered many familial and suprafamilial taxa suspect. Fast on its heels came the more general revolution in taxonomic theory known as cladistics, which not only corroborated the falsehood of the Cribellatae, but undermined confidence in the existing classification (i.e., alleged taxa) even more. By the late 1970s it is fair to say that many workers had realized that two centuries of higher classificatory results were mostly wrong, that no supra-generic grouping in spiders was beyond question, and that most of it would have to be redone or at least checked. In short, the classification of Araneae has lacked any reliable foundation for the last 20 years, despite the hollow superstructure that persisted. This implosion of confidence affects more than mere bookkeeping. Broad generalizations about taxon-based evolutionary or ecological process and pattern are impossible if one's notion of history (i.e., taxa) is awry. As is evident from *Advances in Spider Taxonomy*, arachnologists will now have to get to know major new families such as the Idiopidae (18 genera), Hexathelidae (11 genera), Cyrtaucheniidae (18 genera), Nemesiidae (37 genera), and Orsolobidae (27 genera), as well as major changes in recently recognized families such as

Cyatholipidae (7 genera) and Tetrablemmidae (30 genera). The infraordinal classification of Mygalomorphae is completely new. Old concepts of families such as Agelenidae, Amaurobiidae, Clubionidae, Dictynidae, and Hahniidae have been altered beyond recognition. *Advances in Spider Taxonomy* and some ancillary literature permits the estimate that only about 180 araneomorph genera in 22 or 23 families still contain cribellate species. Because cribellate taxa are likely to be morphological relicts, they become especially important to include in phylogenetic analyses. The comfortable but narrow view of north temperate arachnologists continues to break apart.

Advances in Spider Taxonomy reflects this revolution. Platnick makes it quite clear that the order followed in the catalog does not reflect his personal ideas about spider phylogeny, and he remains uncomfortable with some of the more anomalous groupings that still persist nomenclatorially (will someone PLEASE sink this family?). He wisely dropped Brignoli's effort at subfamily groupings, who in turn wisely dropped Roewer's efforts at supra-familial groupings. Thus all genera within families, and species within genera, are listed alphabetically. The order of families does still follow that of Brignoli, which is to say a one-dimensional representation of presumed phylogenetic order. All in all, the arrangement of *Advances in Spider Taxonomy* is certainly an improvement and more realistic, since users of Roewer's catalog tend to wear out the index faster than anything else.

Despite this retrograde trend of the past few decades, progress has been made in discerning the phylogeny of Araneae (largely due to the taxonomic work of Platnick and collaborators). Mesothelae and Opisthothelae are monophyletic, as are Mygalomorphae and Araneomorphae. Within Araneomorphae two large nested taxa seem valid: Neocribellatae and Araneoclada. From *Advances in Spider Taxonomy* we find that Liphistiomorphae has just two genera, but its sister group (by definition of equal age) has 2942. Mygalomorphae has 259, but its sister group Araneomorphae has 2683. Within Araneomorphae the pattern repeats itself: Paleocribellatae includes only two genera, whereas its sister taxon Neocribellatae has 2681 genera. Finally, Araneoclada has 2671 genera. Obviously diversification rates among spider lineages of equal age are highly dissimilar (assuming that variation in generic size is unbiased). Within Araneoclada, however, few large suprafamilial groupings are supported by competent phylogenetic arguments. One can mention only Dysderoidea (99 genera, 4 families), Palpimanoidea (51 genera, 10 families), Gnaphosoidea (151 genera, 6 families), and Orbiculariae (724 genera, 13 families).

On a more frivolous level, I cannot help but note how this catalog exposes the nomenclatorial foibles of taxonomists. Rendering one's phylogenetic speculations immortal by combining the root of a pre-existing name with a small set of particles (Allo-, Holo-, Meta-, Neo-, Para-, Proto-, Pseudo-, -oides, -iella, etc.) seems irresistible. Like sustained stutters these etymological traditions, once started in a family, are hard to stop. Thus Theraphosidae has always had a bad infection of **pelma* names, Lycosidae had its **osa* names, and Ctenidae was beset with a cacophonous diversity of **ctenus* (with apologies to DOS file-naming conventions). The work this catalog chronicles has not been kind to this sort of ersatz cladistic insinuation. Although *Segestria* cannot avoid being a segestriid, its erstwhile nestmate *Segestrioides* is now a diguetid. *Atypoides* no longer nestles close to *Atypus*. *Neocteniza*, alas, has fled the Ctenizidae for the Idiopidae.

Dysderina and *Dysderoides* turn out to be oonopids. At the other end of the order, the *.*poena* tradition bravely begun in Theridiidae has been largely a mysmenid phenomenon lately; even the patriarch *Dipoena* barely missed expulsion from the Theridiidae (the latter swallowed the Hadrotarsidae instead). Traditions that still endure are the *.*drassus* set in Gnaphosidae, and the *.*nops* crowd in Oonopidae (although a fair number of the latter have broken ranks and fled to the Caponiidae). New beginnings of this sort among leptonetids and palpimanoids show that hope springs eternal. Nevertheless, I am personally relieved that the ranks of *.*osa* in Lycosidae and *.*pelma* in Theraphosidae have been decimated by synonymy. The lesson of history for such semantic allusions (and taxonomic hubris) is clear.

In sum, *Advances in Spider Taxonomy* is a splendid volume. I do not have to recommend that you buy it, because you already know that it is indispensable. Arachnologists and beyond owe Platnick fervent thanks, because few works are as critical to good biology as nomenclatorial catalogs. If taxonomy is the *sina qua non* of all biological science, it is because of works such as this.

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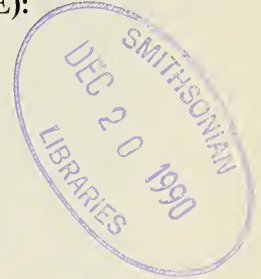
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**DAILY LOCOMOTOR ACTIVITY PATTERNS IN THREE
SPECIES OF *CUPIENNIUS* (ARANEAE, CTENIDAE):
THE MALES ARE THE WANDERING SPIDERS**

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and Friedrich G. Barth**

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ABSTRACT

The daily locomotor activity patterns of spiders of three large species of the genus *Cupiennius* (Ctenidae) were measured in an artificial 12:12 light:dark cycle. Adult males ($N = 10$) and females ($N = 10$) of each species of these nocturnal Central American wandering spiders were compared. On average, males were 3.5 (*C. coccineus* and *C. getazi*) to 12.7 (*C. salei*) times more active than females. Hence, males are the truly wandering spiders. We suggest that this is due to sexually motivated searching behavior of the males. Of the two sympatric species, the males and the females of *C. coccineus* were on average 3.1 times more active than those of *C. getazi*. In addition *C. coccineus* exhibited a relative minimum in its locomotor activity when *C. getazi* showed its absolute maximum. This difference in activity pattern may contribute to the reproductive isolation of these two sympatric species.

INTRODUCTION

In the field adult and subadult wandering spiders of the species *Cupiennius salei* (Keyserling) are quite sedentary. Identified individuals were previously found in their retreats on the same dwelling plants for at least one week (Barth and Seyfarth 1979; Seyfarth 1980). We verified this finding during a recent stay in Central America (Barth, Baurecht, Schmitt, unpubl. data) for *C. salei* and extended its validity to *C. coccineus* F. P.-Cambridge and *C. getazi* Simon. Our general impression, however, was that males of all three species moved around more than the females during their nocturnal activity period.

Vibratory courtship behavior of the males of these three *Cupiennius* species is released by pheromones on the silken threads of females (Rovner and Barth 1981; Barth 1989). Hence, males must find the female silken threads and the females themselves for reproducing. We therefore conjectured that the male might locomote more than the female *Cupiennius*.

C. getazi and *C. coccineus* are sympatric species (Barth et al. 1988). Female pheromones and, more importantly, male vibratory signals contribute to reproductive isolation (Barth 1989). Differences in the daily activity patterns of the two species might be an additional mating barrier between them.

The primary purpose of this study is to delineate the extent to which differences in locomotor activity occur among the sexes and the species. A

valuable byproduct of our measurements are data on the time of day to be chosen for behavioral and physiological experiments.

MATERIAL AND METHODS

Spiders.—All spiders were laboratory bred adult males and females of three large species of Central American nocturnal ctenids: *Cupiennius salei* from Mexico, *C. getazi* and *C. coccineus* from Costa Rica (for general biology and taxonomy see Melchers 1963; Lachmuth et al. 1984; Barth et al. 1988). 20 spiders of each species (10 males and 10 females, all virgins) were used. *C. salei* males were 14.5 ± 1.2 months old (mean \pm SE) and weighed 2.43 ± 0.2 g (mean \pm SE), females were 14.3 ± 1.3 months old and weighed 3.44 ± 0.2 g. The values for *C. coccineus* were 11.8 ± 0.2 months and 1.73 ± 0.1 g for the males and 11.8 ± 0.4 months and 2.92 ± 0.2 g for the females. For *C. getazi*, the corresponding values were 12.5 ± 0.3 months and 0.94 ± 0.1 g for the males and 12.6 ± 0.2 months and 1.5 ± 0.1 g for the females.

Activity measurements.—The activity of each individual spider was measured continuously for 72 hours using an actograph (Animex, Farad type DSEP), the activity registered during one 10 min period being considered as one data point. The actograph was installed in a light-proof room with a 12:12 L:D cycle and a temperature of $25 \pm 1^\circ\text{C}$. These light and temperature conditions are similar to those prevailing in the natural habitat of *Cupiennius* (Barth et al. 1988). All noisy parts of the Animex system were kept outside the experimental room. During the photophase the room was illuminated with fluorescent tubes (Neon-Freon type). The spiders were transferred within their glass jars into this room at least three days before their activity was actually monitored. This time period suffices to entrain *Cupiennius* by an artificial 12:12 L:D cycle (Seyfarth 1980). All spiders were fed four muscid flies once a week on the same day.

During the 72 hours of measurement, the spiders were kept individually in transparent plastic cages (27×20×5 cm). We used one cage for males and another one for females. Between trials, the cages were cleaned. Water was supplied in the cages. During a trial the ceiling of the cage was covered with a wet cloth netting to keep the relative air humidity at $>95\%$ inside the cage, a value often found in the natural habitat of the spiders (Barth et al. 1988). No retreat was provided for the spiders. The cage was shielded from direct illumination of the room and illuminated from outside and 1 m above by a 60 W bulb (Wolfram thread, frosted glass, 2800°K) during the light-on phase. The light intensity inside the cage was 300 Lux. No unusual behavior of the spiders was observed after the three days of encagement.

Calibration.—The Animex system detects the motion of the spider by measuring the disturbance of a magnetic field. Leg movements alone are not detected. The influence of body weight and speed of locomotion of the encaged spider on the measurements was evaluated by the following experiments:

(a) The mean speed during bouts of spontaneous locomotion of males and females, regardless of species varies between 5 and 89 mm/s, averaging 30 mm/s (SD \pm 16 mm/s; $N = 6$, $n = 60$). A narcotized spider was moved on a piece of cardboard by an electrically driven device over a constant distance through the magnetic field of the Animex system at two speeds, of which the first was close to

the above mentioned average (36 mm/s) whereas the second was higher by almost 200% (106 mm/s). This large increase in speed increased the number of impulses registered by only 5%. Thus, this experiment demonstrated that the speed of locomotion of the encaged spider had virtually no influence on the measurements.

(b) Spiders weighing 1 g and 4 g respectively, were moved at the same speed (36 mm/s) through the magnetic field. A spider had to be moved between 26 mm (if 4 g) and 32 mm (if 1 g) to elicit one impulse in the Animex system. Thus, an increase in body weight by 300% increased the number of impulses registered by roughly 23%. We corrected all the data for body weight. Body weight of each spider remained nearly constant during the three days of measurements (weight losses amounted to ca. 3% within one week without food).

The number of impulses registered by the Animex system was transformed into distance (meters) covered by the spider, using the above data.

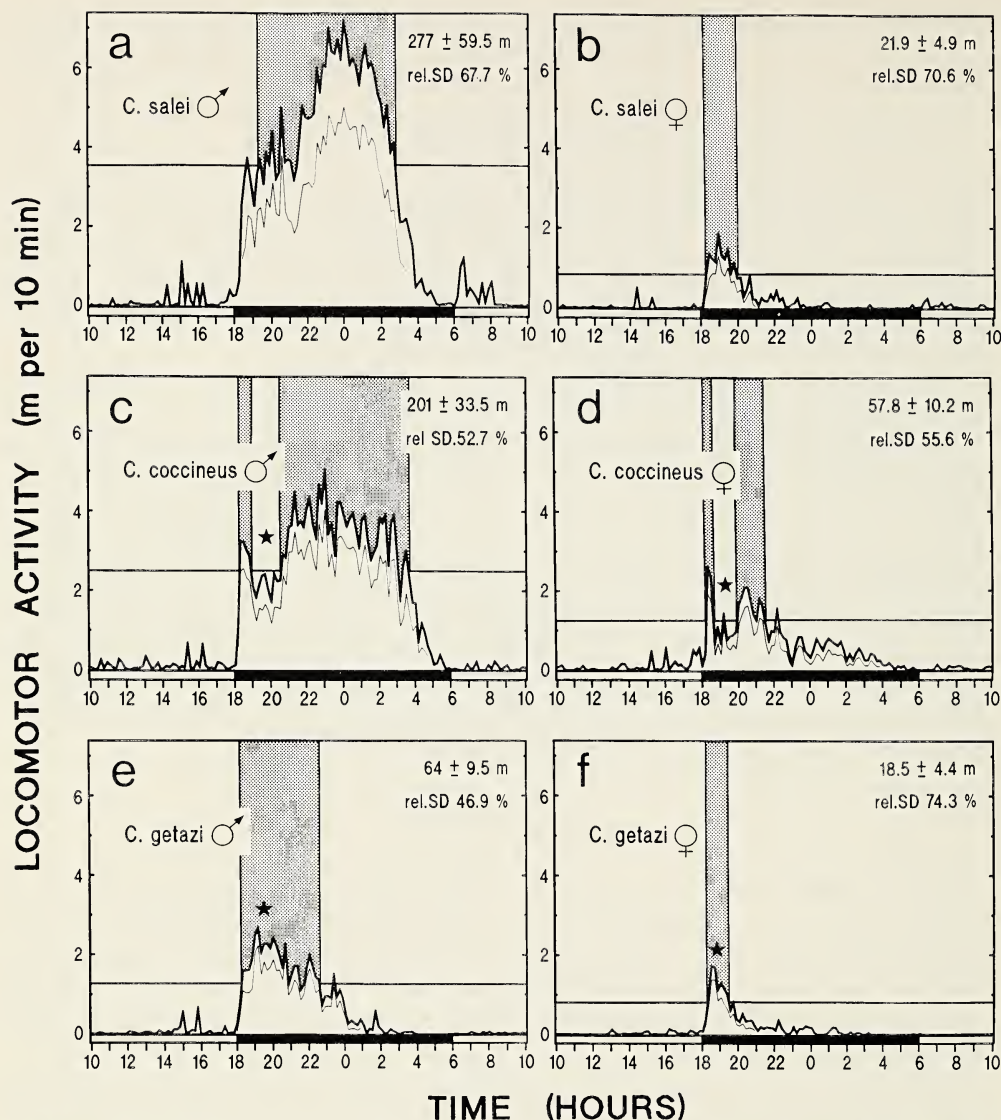
Evaluation of data.—We calculated the total daily amount of activity [given in meters, mean \pm SE and % rel. SD = (SD/mean) \times 100] and determined the duration of the daily activity period and of the period of maximum activity. Periods of maximum activity (dotted areas in Fig. 1) were defined as times of scotophase during which activity of a spider exceeded 50% of the highest value found. All individual data were compared to the mean. They were considered to follow the mean pattern if their period of maximum activity had roughly the same duration (\pm 25%) as the mean and was not shifted by more than 50% of that duration to the left or right on the time axis. Peaks and minima of activity were ignored in this context if they lasted for only 10 min.

RESULTS

The results of the measurements of daily activity patterns of groups of 10 spiders separated by species and sex are presented in Fig. 1. All 20 *C. getazi*, 18 of 20 *C. salei* and 13 of 20 *C. coccineus* showed individual activity patterns very similar to the mean. The interindividual variability in the total amount of activity is large: The rel. SD are between 47% (*C. getazi* males) and 74% (*C. getazi* females, see Fig. 1, insets).

The following comments refer to the mean values. Deviations from them by individual spiders are indicated where necessary.

General features of activity periods.—The data clearly confirm that all three species of *Cupiennius* are nocturnal. Only 4.1% of the total daily activity of the males (average of all species) and 8.7% of that of the females (average of all species) was in the light phase. Activity begins immediately after the lights were extinguished and within 20 min after the onset of darkness, all spiders showed activity values larger than 50% of the absolute maximum values (Fig. 1, 1800–1820). Thus light-off is a very effective Zeitgeber which promptly activates the spiders. Periods of maximum locomotor activity lasted about three times longer in males than in females (in five females of *C. coccineus* the period of maximum activity lasted longer than the average, up to 0200). In both males and females the absolute activity maxima occurred long before the end of the dark phase. The decline was more abrupt in the male *C. salei* and *C. coccineus* than in females of all three species and in the males of *C. getazi*.



Figures 1a-f.—Daily locomotor activity patterns of adult male and female spiders of the genus *Cupiennius* (in all cases $N = 10$); mean (thick line) and standard error (thin line; only lower limits are shown). The total amount of activity (m) is given by the numbers in the right upper corner (mean, standard error and relative SD). Horizontal lines indicate 50% of maximum activity. Shaded areas represent time periods of maximum activity. Star marks time of maximum activity in *C. getazi* and of relative minimum in *C. coccineus*. Black area on time axis indicates dark period (1800 to 0600).

Interestingly, both male and female *C. coccineus* became relatively inactive at the same time during the dark phase, i.e. between about 1900 and 2000 (see star in Fig. 1c,d). After 1-2 h they resumed activity to almost the same degree as at the onset of the scotophase.

The time course of the activity of adult *C. salei* females in our present experiments was similar to that previously reported by Seyfarth (1980) for subadult females of the same species. As is known from Seyfarth's (1980) experiments, this activity pattern reflects a biorhythm.

Differences between the sexes.—The average total amount of locomotor activity of males was 3.5 (*C. coccineus* and *C. getazi*) and 12.7 (*C. salei*) times larger than that of females (Fig. 1). Periods of female maximum activity fell within the periods of maximum male activity (Fig. 1). However, the males of *C. getazi* continued to move around at a high rate for about 4 hours and those of *C. salei* and *C. coccineus* for about 7 hours after the end of the period of female maximum activity (Fig. 1).

The following deviations of individuals of *C. coccineus* from the mean *C. coccineus* activity patterns were observed. Three of the *females* exhibited 5 to 8 activity maxima with zero activity in between instead of a relative minimum at the usual time between about 1900 and 2000. The four exceptional *males*, on the other hand, had their locomotor activity evenly distributed between about 1800 and 0400.

Differences between sympatric species.—The activity periods of the two sympatric species, *C. coccineus* and *C. getazi*, partly overlap, i.e., there was no allochrony (Fig. 1c-f). Apart from the fact that *C. coccineus* males and females were on average 3.1 times more active than *C. getazi* males and females, three remarkable features of the activity patterns of these two species emerge.

(i) *C. getazi* males and females had their absolute activity maxima between 1830 and 2230 and between 1830 and 1930, respectively (star in Fig. 1e,f). During the same time period, *C. coccineus* males (1900 to 2030) and females (1830 to 2000) exhibit a relative minimum in their activity patterns (star in Fig. 1c,d). Absolute activity values of both species were similar during that time period (for exceptions see preceding section).

(ii) The activity of *C. coccineus* males is distributed over nearly the whole dark phase of 12 hours (but see relative minimum, above), whereas *C. getazi* males are only active during the first 8 hours of the dark phase. Correspondingly, the female activities last longer in *C. coccineus* (from about 1800 to 0200, but see minimum, above) than in *C. getazi* (about 1800 to 0200).

(iii) *C. coccineus* spiders were most active when the activity of *C. getazi* was already decreasing (Fig. 1c-f).

DISCUSSION

There are several studies on biorhythms of spiders which have been the subject of a recent review by Cloudsley-Thompson (1987). To our knowledge, however, so far no data are in the literature on sex-related differences in the amount of locomotor activity. Likewise, no comparative data on the activity patterns of closely related spider species are available.

Differences between the sexes.—Field observations on population structure and laboratory studies on courtship behavior of *Cupiennius* (Rovner and Barth 1981; Barth 1989) suggest that sexually motivated searching behavior is the main factor causing the differences in amount of locomotor activity between males and females. Antipredatory behavior and search for prey or a retreat might be additional or alternative factors influencing locomotor activity. The following arguments are considered as evidence against their importance in the given context.

(i) *Predators*: The spiders were not exposed to predators nor disturbed by any obvious stimuli from outside during the measurements. Even if unnoticed stimuli would have been present, they should have influenced males and females in a similar way and therefore cannot account for the observed differences between the sexes.

(ii) *Search for prey*: All spiders were fed according to the same regime with no feeding during the time of measurements. *Cupiennius* is a sit-and-wait predator (Melchers 1963; Barth and Seyfarth 1979). The spiders of all three species come out of the retreat at dusk as first described by Barth and Seyfarth (1979), and, as a rule, move less than one meter on their dwelling plant (pers. obs. Barth, Baurecht, Schmitt). There are no known differences in predatory behavior between males and females. There is no indication that the search for prey could account for the differences in locomotor activity between the sexes.

(iii) *Retreats*: Retreats of the females are often found to be partly or completely closed by compact web sheets. This is never observed for males, neither in the laboratory nor in the field. Females build their egg sacs and take care of them for about three weeks while in their retreats. Spiderlings often hatch within the retreat and live there for about one week before they disperse. We assume that retreats are more important for females and that they might therefore search more intensively for adequate retreats than males when held in barren cages. Despite the complete absence of retreats in the cages, the males were the much more active sex.

Differences between sympatric species.—The number of interspecific encounters in sympatric species is not only determined by their spatial proximity or distance and by their absolute amount of activity, but also by the degree of temporal overlap of their activity periods.

Our data suggest that activity patterns may indeed contribute to reproductive isolation of the two sympatric species, *C. coccineus* and *C. getazi*. The probability of encountering each other is reduced because (i) *C. coccineus* has a relative minimum during the time period of the absolute activity maximum of *C. getazi* and (ii) *C. coccineus* is most active when the activity of *C. getazi* is already decreasing.

The few individual deviations from mean activity patterns do not weaken the above conclusions since temporal isolation has to be considered as a parameter describing two or more groups of individuals (populations) and not single individuals. Thus, mean (population) patterns have to be compared.

Differences in the amount of activity among the three species.—Interspecific differences in total amounts of activity are hard to interpret with the limited knowledge at hand. They could reflect differences in population density, the males of the species with greater population density being less active because of higher chances for finding a female. Data from our field work show, however, that, given similarly high dwelling plant densities, population densities of the three *Cupiennius* species are similar (Barth, Baurecht, Schmitt in prep.).

The rather high absolute values of total amount of activity found in our experiments should not simply be transferred to the primary forest situation. We instead suggest that the activity was particularly high in our cage situation because of the unattractive environment with no retreat, no prey, no sexual partner and no dwelling plant.

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SOME ASPECTS OF THE REPRODUCTIVE BEHAVIOR OF *LYCOSA TARENTULA FASCIIVENTRIS* (ARANEAE, LYCOSIDAE)

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ABSTRACT

The duration of the reproductive and courtship periods, the number of individual matings, and the number of egg sacs and their viability were measured in *Lycosa tarentula fasciiventris* under laboratory conditions. We found that the reproductive period is very short, lasting for a month from July to August. Both the males and the females can mate more than once. Female receptivity is related to age and reproductive state: receptivity is less in both old and previously mated females. Neither the size nor the viability of cocoons is related to the number of female matings. Our results are interpreted in relation to optimization of egg fertilization.

RESUMEN

En *Lycosa tarentula fasciiventris*, hemos medido la duración del periodo reproductivo y del cortejo, el número de apareamientos de cada individuo, el número de puestas de cada hembra y su viabilidad en el laboratorio. Hemos encontrado que el periodo reproductivo es muy breve, de alrededor de un mes, comprendido entre julio y agosto. Tanto los machos como las hembras se aparean más de una vez, estando relacionada la receptividad de la hembra con su edad y con su estado reproductivo: tanto las hembras "viejas" como las previamente apareadas muestran una receptividad menor. Ni el tamaño ni la viabilidad de la puesta están relacionados con el número de apareamientos realizados por la hembra. Nuestros resultados se interpretan en relación a la optimización de la fertilización de los huevos.

INTRODUCTION

Theoretical models which try to explain the reproductive tactics of males and females have been developed which usually refer to species in which both the number of eggs produced by females and the investment of the male in the offspring are very low (Gould 1982; Huntingford & Turner 1987). It has been predicted that females will try to invest in only a few matings, will take less advantage of multiple mating, and will choose the male with which to mate (Halliday 1983, 1986; Huntingford & Turner 1987), whereas males will compete for females.

Lycosa tarentula fasciiventris Dufour is a burrowing spider from the Iberian peninsula. In central Spain, populations are distributed in open and arid areas (Barrientos 1978) with poor plant cover. Temperature conditions are greatly

variable, both seasonally and daily. Animals live in burrows throughout all their developmental stages, except the adult males, with adult females showing the greatest location stability (pers. obs.). Individual development takes place over a period of about 22 months, and animals reach their adult instar at about the end of spring in their second year of life. Reproduction takes place shortly after, at the beginning of the summer (pers. obs.). During this time, males are found wandering in search of females in areas in which isolated individuals are very distant from one another. Male survival after the reproductive period is nil, whereas females may survive for several months. Under laboratory conditions, males may live as long as 2 or 3 months after summer, while females may live as much as 1.5 to 2 years. Like many other spider species (Fink 1986), females show a kind of behavior towards their egg sac that has been called "maternal" (Horel & Krafft 1986). They carry with them both their egg sac and their spiderlings, thus leading to changes in female responsiveness (pers. obs.).

The interindividual distances will make the chance of finding a mate low for both the males and females. Under these conditions, males might be expected to compete for females. However, laboratory observations have shown male agonistic interactions being settled in a ritualized way and leading to apparently paradoxical results (smaller or intruder male wins). Given the fact that female longevity is higher, postcopulatory guarding behavior is not to be predicted (Austad 1984). Competition between females might also be expected (Fernández-Montraveta & Ortega, in press), as well as female choice, given that female investment is greater than in the male.

In this paper we try to measure some reproductive behavior variables in order to evaluate how they fit the expected patterns according to whether or not animals are behaving in ways that lead to relatively high reproductive payoffs.

MATERIAL AND METHODS

In this study, 71 adult males and 66 adult females were used. All the animals were from the countryside around the "Universidad Autónoma de Madrid". All the males and 56 females were collected during the spring of 1985 and 1986, when immature, usually at their penultimate developmental stage. The remaining females (10) were collected as adults around the end of winter, 1985. Animals were kept isolated under controlled conditions of temperature ($25 \pm 5^\circ\text{C}$), 10:14 light:dark cycle, and fed twice weekly with a blowfly outside the observation periods.

Animals were observed in their adult stage. The observation chamber was a terrarium occupied both by the male and the female for a week before the observation took place. Previous to the observation, animals were visually isolated from one another; the partition was removed to carry out the observation. We used only males having molted to adults during the year of the study, 37 females having also molted during this year ("young females") and 29 adult females 1 year old when the observation took place ("old females"). This last group comprised both the animals collected when adults, presumably "copulated females", and animals collected when immature that have not copulated during their first adult year ("virgin females"). The decision to consider the first group of females as copulated ones was made *a posteriori*: all of these animals later constructed a viable egg sac, without copulating, in the laboratory.

During July and August of both 1985 and 1986, we observed 254 pairs of animals. Pairs were formed at random with regard to individual variables. Every animal was observed at first through the first week after molting, and at least twice on different days. If copulation occurred, the second observation was made during the first week after copulation and so on. Each observation lasted at least 30 min. Females were usually inside their burrow, so interaction took place there. We have considered that interaction began when the male was 2 or 3 cm away from the female burrow, and oriented towards it. When an interaction took place, the observation was prolonged as long as it lasted. Interaction finished when the male moved away from the female nest and ceased orientation. Ninety-five interaction sequences were obtained and analyzed. After the observation period, animals were kept in the laboratory and observations about the subsequent reproductive activity were made.

We measured (i) the date on which molting to adulthood took place, (ii) the date of copulation, (iii) the result (copulation/retreating before copulation) of interactions, (iv) the number of matings for both sexes, (v) the courtship and copulation durations, (vi) the number of egg sacs for every female, (vii) the weight of each egg sac and (viii) the number of spiderlings emerging from each egg sac. Results have been compared with regard to four female groups, two related to female age (young females/old females) and the other related to their previous reproductive history (virgin female/copulated female).

As for quantitative variables, their mean values and standard deviations have been calculated. In order to compare the means, a variance homogeneity test was made before applying the *t*-test.

In order to measure how the quantitative variables are related, the correlation coefficient was calculated and the Chi-square test was applied to measure the independence of the results with regard to the different female groups.

RESULTS

In 1986, both male and female molting in the laboratory reached a peak about the second week of June. In 1985, the same peak was observed about the third week of June in males and the second week of July in females. Copulation was observed from the middle of June to the first week of August, and the copulation rate increased steadily with time. Peaks were observed at the end of July (1986) and the beginning of August (1985).

Forty-six copulations were observed in all. When in the second year of their adult life, only 42% of the females were receptive if virgin, as contrasted to 81% of the young virgin females. The old, previously mated females were not receptive at all (Table 1). We tested the dependence between receptivity and "age" and "previous reproductive history" separately. Female receptivity significantly depends on the female's previous reproductive history ($\chi^2 = 5.53$, $p < 0.05$); virgin females were receptive in 68% of the cases in contrast to 39% of the previously copulated females. It also depends significantly on age ($\chi^2 = 19.80$, $p < 0.05$); 78% of the females were receptive when young and only 28% when old.

Forty-eight per cent of the males observed succeeded in copulating, in contrast to 68% of the females. Both the males and the females can mate more than once under laboratory conditions (Table 2). Sixty-five percent of the males copulated

Table 1.—Female receptive response to mating with regard to its age and its previous reproductive history (PRH).

Variable		Receptive Response		Total
PRH	Age	Yes	No	
Virgin	young	30	7	37
	old	8	11	19
Copulated	young	8	5	13
	old	0	10	10
Total		46	33	79

once and 35% twice, but no male copulated more than twice. Among the females, 82% were receptive only once, 16% twice and 3% more than twice.

Mean courtship duration was 23.4 ± 21.25 min. The mean duration when the courted female was virgin, regardless of age, was 17.6 ± 17.34 min. The mean courtship duration when females were young virgins was 20.1 ± 20.35 min, and 15.3 ± 13.70 min when old virgins ($t = 0.42$, ns). The mean courtship duration when the female was young and had previously copulated was 25.0 ± 16.26 min and 40.7 ± 28.77 min when the courted females were old, previously copulated ones. There is a statistically significant difference between the mean courtship duration of the virgin group, regardless of age, and the old, previously copulated group ($t = 2.14$, $p < 0.05$). The observed mean copulation duration was 89.2 ± 31.1 min.

Data from 35 first egg sacs were analyzed. Of these, 30 were from females having copulated once and five from females having copulated twice or more. Mean weight of the egg sacs was 0.30 ± 0.10 g in the first group and 0.22 ± 0.06 g in the second ($t = 1.60$, ns). We observed no greater size in the egg sacs of females that copulated more than once. Spiderlings emerged from 21 egg sacs in the first case and three in the second. Mean number of emerged spiderlings was 117.2 ± 51.8 in the first group, and 105.67 ± 31.41 in the second. The correlation coefficient between egg sac weight and number of living spiderlings was 0.61 ($p < 0.05$).

There were 20 second egg sacs, both by females collected as adults and by females kept in the laboratory for more than 1 year. The second egg sac was then produced in the second year the females lived, not being preceded by mating during that year. Living spiderlings emerged from 10 of them (50%).

DISCUSSION

We measured some synchronization between the molting dates of males and females, providing mating is concentrated during a very short period of time. We

Table 2.—Number of males and females copulating once, twice, or more than twice.

Sex	Number of matings			Total
	1	2	>2	
Male	22	12	0	34
Female	31	6	1	38
Total	53	18	1	72

consider that the difference observed between the two years might indicate that the individual molting date is adjusted to the changing environmental factors. Since animals for the most part were captured shortly before their molt to adults, we think these factors could have affected individual molting dates.

The nature of the factors determining female receptivity, related to its age and previous reproductive history, might explain the observed shortness of the period in which mating took place. This time limitation suggests that competition between males is reflected in their early maturation rather than by direct aggression, accounting for the earlier maturation peak shown by males, especially in our first year of study. This hypothesis might also explain the apparently paradoxical resolution of male interactions we observed in this species.

Both the males and the females we observed can achieve more than one mating, as do many other spider species (Jackson 1979; Austad 1984; Christenson 1984; Breene & Sweet 1985; Brown 1985). Our results do not suggest multiple mating to be related to greater success of the first female egg sac in this species. Since sexual partners seem to be limited, the multiple-mating benefit for females might be related to the sperm supply (Austad 1984; Christenson 1984), given the egg sac size and the need for sperm to be stored in order to be successively used (Christenson et al. 1985). The greater cost of rejecting a persistent male rather than accepting copulation as the reason for this multiple mating (Austad 1984; Christenson et al. 1985) does not seem to be the most appropriate explanation because non-receptive females of this species are rather aggressive (Ortega et al. 1986), like other lycosid females (Rovner 1972). The need for a sperm supply, along with the possible benefit of genetic diversity among offspring (Christenson 1984; Huntingford 1984; Huntingford & Turner 1987) could be the reason why female reproductive strategy consists of accepting matings with several males during one reproductive period.

Female sperm storage, as well as multiple egg sacs seems to be a general pattern in spiders (Austad 1984; Christenson 1984; Blandin & Célériér 1986; Fink 1986). Mating also takes place before the first oviposition in other spider species (Austad 1984; Sadana pers. com.). The advantages of this species concentration of mating in only one reproductive period should be explored. We think this concentration might be a consequence of the great seasonal climatic differences, given the lesser inter-egg sac period shown by other lycosid spiders.

Since, in the species we have studied, female investment is greater than the male's, female choice should be expected (Huntingford 1984). With regard to the kind of individuals with which a female mates, its behavior when virgin does not seem to be discriminative (Ortega et al. 1986). Female choice has been postulated in a few cases (Austad & Thornhill 1986), as taking place when females have already copulated (Jackson 1982). This is interpreted as first mating guaranteeing egg fertilization, offspring quality being increased in the following matings (Halliday 1983). The occurrence of multiple mating with lesser receptivity of previously mated females agrees with that prediction.

The duration of male courtship with regard to female reproductive status might indicate male behavior is based on investing a fair amount of time courting every female found, even if she does not show any receptive response at first (Ortega et al. 1986).

To reach the adult stage early and to succeed in mating with all the females he finds would define the male reproductive tactic. Females, on the other hand, will

try to choose the male to mate with after the sperm supply has been guaranteed, and to reduce the copulation duration to the effective insemination period. Conflict of interests will arise over these factors. Males are expected to prolong the copulation duration beyond the effectiveness of insemination, whereas females are expected to try to reduce the total copulation duration to just the effective insemination periods. More data on copulation in this species is needed to test this hypothesis.

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DETERMINANTS OF FECUNDITY IN *FRONTINELLA PYRAMITELA* (ARANEAE, LINYPHIIDAE)

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ABSTRACT

The fitness of *Frontinella pyramitela* (Walckenaer) (Araneae, Linyphiidae) is, by definition, a function of its lifetime fecundity and the survivorship of its offspring. In the present study, I sought the major determinants of fecundity in a laboratory setting and then evaluated the results in the context of several published field studies. According to this analysis, the primary determinants are female longevity, foraging success, and size. The data also permitted the calculation of an expected relative contribution to total fecundity of each clutch of eggs: because the fertility rate drops sharply after the second clutch is deposited, early mortality is disproportionately detrimental to lifetime fecundity.

INTRODUCTION

Darwinian fitness, despite its succinct definition, is notoriously difficult to assess in living organisms (Endler 1986) because three of its principal components, age at first reproduction, lifetime fecundity, and survivorship of offspring (Vehrencamp and Bradbury 1984; Horn and Rubenstein 1984), can seldom all be measured. Nevertheless, differences among animals in any one component are likely to be strongly correlated with differences in fitness, and thus it has become common to study fecundity (number of live births), for example, as an index of fitness (e.g., Emlen and Wrege 1988; Riechert and Tracy 1975).

Scattered in the arachnological literature are numerous reports on aspects of spider fecundity such as eggs per clutch, time between clutches, and fertility. The earlier studies have been reviewed by Turnbull (1973). In more recent literature, a number of authors have reported that ecological variables such as photoperiod (Miyashita 1987a) or foraging success (Riechert and Tracy 1975; Wise 1979; Morse and Fritz 1987), and individual variables such as female size (Fritz and Morse 1985; Killebrew and Ford 1985), contribute to observed intraspecific variability in spider fecundity. Other reports, taken together, have demonstrated the plurality of spider responses to ecological variables: ambient temperature appears not to influence fecundity in one theridiid, *Achaearanea tepidariorum* (C. L. Koch) (Miyashita 1987b), but has a strong influence in another, *Theridion rufipes* Bryant (Downes 1988); similarly, food deprivation does not affect the number of eggs produced either by a linyphiid, *Linyphia triangularis* (Clerck) (Turnbull 1962), or by some species of the lycosid genus *Pardosa* (Kessler 1971),

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but it does affect the number of eggs produced by other *Pardosa* species (Kessler 1971) and by a thomisid, *Misumena vatia* (Clerck) (Fritz and Morse 1985). This variety of responses to the same environmental variables suggests that it may be unwise to generalize (Eberhard 1979).

In the laboratory investigation reported below, I attempted to discover the primary determinants of fecundity in the bowl and doily spider, *Frontinella pyramitela* (Walckenaer) (Linyphiidae). This spider is a small, nearly ubiquitous inhabitant of fields and shrublands in temperate North America. It has been the subject of numerous ecological (e.g., Janetos 1983; Suter 1985), ethological (e.g., Hodge 1987; Austad 1983; Suter and Parkhill 1990), and biophysical (e.g., Pointing 1965; Suter 1984; Suter et al. 1987) investigations.

MATERIALS AND METHODS

In May of 1988 I captured immature male and female *F. pyramitela* from their webs in old fields in Dutchess County, NY. The spiders were reared to adulthood in isolation from their conspecifics in 473-ml plastic containers at 100% RH, approximately 12:12 photoperiod, and 22–24 °C. They were maintained on a diet of live vinegar flies (*Drosophila melanogaster*), and mean feeding rates varied between 0.62 and 1.55 flies per day (0.81 to 2.02 mg/d). The variation was attributable in part to the spiders' prey capture success and in part to an interaction between the feeding schedule and the timing of ovipositions (feeding is inhibited for 1 to 2 days prior to oviposition). The range of feeding rates brackets Austad's (1989) field estimate of foraging success (1.48 mg/d, equivalent to eight *D. melanogaster* per week) and is lower than my own direct field measure of foraging success (Suter 1985: median = 3.12 mg/d). Females were virgins at the beginning of the study and were allowed only a single mating which occurred within 7 days of the molt to adulthood.

I recorded the matings on videotape (at 2 fps) and then removed the males. The videotaped images provided accurate information about the duration of the insemination phase (Austad 1982; Suter and Parkhill 1990) of each mating. Females that deposited eggs fertilized in those matings ($N = 57$) were transferred to new containers after each oviposition, and their egg cocoons ($N = 169$) were maintained under the conditions outlined above. Egg cocoons were transferred to 70% ethyl alcohol eleven days after oviposition and subsequently analyzed with respect to number of progeny (well-developed eggs or hatched spiderlings), size of progeny (Suter and Parkhill 1990), and unfertilized eggs (no visible evidence of tissue differentiation).

Fourteen pairwise relationships among the variables were evaluated using regression statistics, with $\alpha = 0.01$ because of the large number of tests. The resulting probabilities were used not to reject explicit hypotheses but rather as a guide to important relationships. Multiple regression of copulation duration, number of clutches, and female mass on lifetime fecundity was not performed because the number of females on which all three independent variables were available was small (18).

Table 1.—Components of fecundity in *F. pyramitela*. Number of progeny, latency to oviposition, and productivity were tested for relationships with other variables. For those comparisons in which the coefficient of determination was significant ($P < 0.01$), the sign of the slope of the tested line is indicated in parentheses.

Relationship	<i>N</i>	r^2	<i>P</i>
Total progeny versus copulation duration (see Suter and Parkhill 1990)	40	0.004	0.742
Total progeny versus total number of clutches	55	0.458 (+)	< 0.001
Progeny per clutch versus post-oviposition mass of female	24	0.348 (+)	0.001
Progeny (I) versus feeding rate (flies/day between insemination and first oviposition)	50	0.263 (+)	< 0.001
Progeny (II) versus feeding rate (flies/day between first and second ovipositions)	50	0.314 (+)	< 0.001
Progeny (II) versus latency (II) (second oviposition data only)	50	0.110	0.020
Latency (I) versus food consumption (time and flies consumed between insemination and first oviposition)	51	0.037	0.179
Latency (I) versus post-oviposition mass of female	23	0.282 (+)	0.004
Latency (II) versus food consumption (time and flies consumed between first and second ovipositions)	51	0.136 (+)	0.008
Latency (II) versus post-oviposition mass	28	0.009	0.637
Latency (III) versus food consumption (time from insemination, flies between last molt and first oviposition)	49	0.038	0.182
Eggs per clutch versus clutch order	169	0.365 (—)	< 0.001
Productivity (I, eggs/feeding rate) versus post-oviposition mass of female	24	0.005	0.972
Productivity (II, eggs/feeding rate) versus post-oviposition mass of female	27	0.067	0.181

RESULTS

The results of this study are summarized in Table 1. Of the 14 relationships tested, six were significant ($P < 0.01$) and had positive slopes. (1) Spiders that lived for many weeks after insemination produced more clutches, and consequently more live progeny, than did spiders that died soon after insemination. Figure 1 characterizes the variation in this relationship between total fecundity and number of clutches produced. (2, 3) The feeding rate achieved by a female strongly affected the number of progeny produced in the immediately succeeding clutch for both the first and second clutches. (4) The number of live progeny in each clutch was strongly related to the mass of the female after oviposition. (5) Larger female mass also increased the delay between insemination and first oviposition, but mass differences were not related to differences in the latency to the second oviposition. (6) Latency to the second oviposition was strongly related to food consumption during the same period, an uninteresting

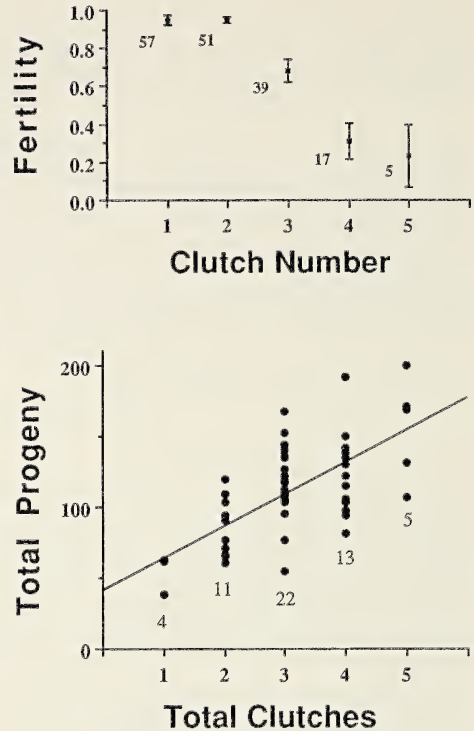


Figure 1.—The fecundity of bowl and doily spiders (lower panel) is closely tied to the number of clutches produced ($r^2 = 0.458$), which is in turn closely related to longevity. This relationship exists despite the rapid decrease in fertility that occurs after the second clutch is deposited (upper panel, and see Suter and Parkhill 1990). Much of the variation seen in the lower panel is probably attributable to the consequences of differences among females in mass and food consumption (Table 1).

consequence of the fact that animals with shorter latencies had fewer days during which to capture prey.

One other relationship was significant but had a negative slope: (7) With respect to number of eggs per clutch, earlier clutches contained more eggs than did later clutches (ANOVA, $F = 5.97$, $P < 0.001$) although most of that variation was due to higher numbers in first clutches (mean \pm SD clutch size for all clutches, 42.12 ± 14.40 , $N = 169$; for first clutches, 53.32 ± 14.37 , $N = 57$; Bonferroni simultaneous confidence intervals for all comparisons in the ANOVA show that only the first clutch is significantly different, at the 0.05 level, from the grand mean). This relationship was previously reported for this species by Austad (1982, 1989).

The latency to oviposition for the first clutch (I) was measured from the date of insemination whereas the latency to oviposition for the second clutch (II) was measured from the date of the first oviposition. It is perhaps not surprising, therefore, to find that latency I was significantly shorter than latency II (I, mean \pm SD, 9.62 ± 3.2 , $N = 47$; II, 11.83 ± 3.26 , $N = 47$; $t = 3.41$, $P = 0.001$), because a female probably begins to synthesize yolk prior to insemination. Similarly, productivity (measured as eggs produced relative to the food intake rate), is lower for the second clutch than for the first, probably because the first clutch contains some pre-insemination yolk [first, mean \pm SD, 50.51 ± 14.42 eggs/(flies/day), $N \pm 47$; second, 39.01 ± 12.99 , $N = 54$; $t = 4.44$, $P < 0.0001$].

Eggs per clutch varied linearly with feeding rate over the range of feeding rates (0.81 to 2.02 mg/d) in this study, with a slope of 32 eggs/(mg/d). Thus over the mean 11.8 days between clutches, a spider could produce about 2.7 eggs per mg of prey mass consumed.

DISCUSSION

The data presented above elucidate the primary determinants of lifetime fecundity in *F. pyramitela* in a laboratory setting: longevity, size, and feeding rate.

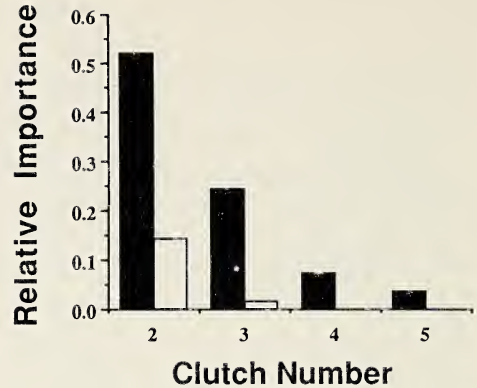
Longevity.—Animals that live longer have more opportunities to reproduce, usually, than those that live only briefly. In animals that reproduce repeatedly, lifetime fecundity is particularly sensitive to variation in survivorship. Because the bowl and doily spider is iteroparous, it is not surprising to find that females that live longer produce more clutches and more eggs (Fig. 1, Table 1). In the laboratory, these spiders deposit up to five clutches containing about 42 eggs per clutch [approximately twice the clutch size reported by Austad (1982), but very close to field reports by Austad (1989)] at approximately 11-day intervals. Fertility declines rapidly after the second clutch (Fig. 1) although egg production does not. The sharp decline in fertility after the second clutch (also reported by Austad 1982, 1989) may indicate sperm depletion or senescence, egg senescence, or some combination of these factors.

The implications of these data can be assessed in the context of field survivorship of *F. pyramitela*. Austad (1989) has reported that in field studies, females have surprisingly high mortality rates: his data indicate losses equivalent to 13.5% of the population per day (a probability of mortality of 0.135 per adult female per day). The estimate is about four times higher than my own calculations (0.035 per adult female per day, unpublished data) based on a field demographic study (Suter 1985). Using as bases for calculations the average oviposition latencies reported above and mortality rates of 0.135 (Austad) and 0.035 (Suter), the proportion of females surviving to deposit clutches one through five would be 0.248, 0.045, 0.008, 0.001, and 0.0002 (Austad) and 0.710, 0.466, 0.305, 0.200, and 0.131 (Suter). An estimate of the expected relative contribution of each clutch to lifetime fecundity can be derived from the product of the survivorship probability and the expected number of live young (mean fertility \times mean clutch size). Those expected relative contributions, shown in Fig. 2, confirm that longevity, particularly through the first two clutches, is crucial as a determinant of lifetime fecundity in *F. pyramitela*.

Size.—Prior to the present study, size variation in *F. pyramitela* was already known to be important in determining the outcomes of agonistic contests both between males (Austad 1983; Suter and Keiley 1984) and between females (Hodge 1987). The data reported above indicate that mass also contributes directly to fecundity per clutch (Table 1, Fig. 1), as it does in many other invertebrates. Thus larger females of this species benefit because (1) their clutches are larger, (2) they retain possession of their webs more frequently (Hodge 1987), (3) they capture more prey biomass per unit time (Janetos 1983), and (4) they may have a somewhat greater resistance to desiccation and other environmental challenges. [The determinants of adult size in this species have not been explored but are obviously important contributors to fitness. Presumably both size at hatching (Suter and Parkhill 1990) and food availability, as well as genotype, are involved.]

Foraging success.—Because nutrients are required to produce the yolk that is the primary constituent of spider eggs, the positive relationship between feeding rate and fecundity, and the negative relationship between feeding rate and latency to oviposition, are expected. The relationships probably reflect reality under field

Figure 2.—The expected relative contribution to lifetime fecundity of each clutch. The measure is the product of the probability that the female will survive to oviposit and the expected number of live young (clutch fertility X clutch size) in the clutch, all set relative to the first clutch (1.0). The filled bars are based in part upon an estimate of female mortality (0.035/day) from Suter (1985); the open bars are based upon an estimate of mortality (0.135) derived from Austad (1989).



conditions: clutch sizes and latencies are comparable to those reported by Austad (1989) and the feeding rates in the laboratory are representative of field conditions (Austad 1989; Suter 1985). Both relationships confirm the findings of Austad (1989) and indicate a positive contribution of foraging success to lifetime fecundity. Because feeding rates in this study were not systematically manipulated, however, the range of rates was relatively narrow. I propose to explore the upper limits of food intake in this species to look for both clutch mass and egg number constraints. Such a study would make possible a comparison with the interesting report by Riechert and Tracy (1975) that there is a limit to the number of eggs produced by the agelenid, *Agelenopsis aperta* (Gertsch), but no limit to the total mass of eggs produced.

Janetos (1983) has shown that larger *F. pyramitela* capture larger prey, on average, than do smaller ones. If this relationship holds for all sizes and instars, then larger hatchlings (Suter and Parkhill 1990) would become among the largest of adults and have all of the other advantages of large size to which I alluded above. Clearly a female's foraging success and her size reinforce each other in ways that ultimately augment fecundity.

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POTENTIAL LIFETIME FECUNDITY AND THE FACTORS AFFECTING ANNUAL FECUNDITY IN *URODACUS ARMATUS* (SCORPIONES, SCORPIONIDAE)

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ABSTRACT

The ovariuterus of *Urodacus armatus* had three types of diverticula, Rudimentary (RD), Embryonic (ED) and Post Partum (PPD). The data suggested that all the ova were developed and enclosed in RDs by the time a female reached maturity and that the sum of the diverticula gave a measure of the potential lifetime fecundity. Samples from two populations in two consecutive years were not significantly different and the combined mean for all diverticula was 56.7 ± 8.22 .

Annual fecundity (number of EDs) did not differ between populations or years and the combined mean was 8.3 (range 4-12). Fecundity was not significantly influenced by female condition ($\sqrt[3]{\text{Mass/carapace length}}$), length of ovariuterus or the total number of diverticula. However, size and age had significant effects. The simplest adequate model explaining the variation was given by the equation $\log \text{ED} = 0.9656 - 0.07003 \text{ Age} + 0.01839 \text{ Carapace length}$. Data on age-related fecundity and total diverticula suggested that females may have from 5 to 12 litters in a lifetime.

INTRODUCTION

Studies on a variety of invertebrates have shown that fecundity can be influenced by a number of variables: size, (Juliano 1985; King 1987; Banks and Thompson 1987; Haack et al. 1987); population density, (Wise 1975; Banks and Thompson 1987); food, (Wise 1975; Riechert and Tracey 1975; Haack et al. 1987); age, (Ribi and Gebhardt 1986); temperature, (Baird et al. 1987); geographic location, (Hines 1982; Davies 1987; Atkinson and Begon 1987; Ribi and Gebhardt 1986); size of egg or offspring, (Ribi and Gebhardt 1986); size of male ejaculate, (Svård and Wiklund 1988); number of previous matings by male, (Rutowski et al. 1987), and clutch interval, (Banks and Thompson 1987). The variables that affect fecundity in individual species differ as do the direction of the effect and the degree of interaction with one another. Size, for most species, is the dominant variable either directly or indirectly via its effect on other variables affecting fecundity. Lifetime fecundity or reproductive success has been studied in only a few species (Banks and Thompson 1987; Fincke 1987; Koenig and Albano 1987; Svård and Wiklund 1988). In addition to the variables that affect individual breeding events, lifetime fecundity will be affected by the length of reproductive life, number of clutches and variables associated with the male. The majority of the above studies are on short-lived, oviparous species; there have been no studies on long-lived viviparous invertebrates.

Most data on reproductive rates in scorpions are measures of fertility (number of live births) obtained from specimens in captivity or animals in the field (Polis and Farley 1979), and both methods may give values less than the true reproductive rate. Captive specimens, depending on the time spent in captivity may have more abortions, suffer from maternal cannibalism or displacement of young from the mother's back and may fail to shed the birth membrane (Polis and Farley 1979). Similar mortality factors also operate on litters in the field but have not been directly observed (Smith 1966; Polis and Farley 1979).

In viviparous animals, such as scorpions, no methods have been developed to attain data on fecundity (number of fertilized ova) without sacrificing the animal. However, in detailed studies on population dynamics and life history strategies, it is important to have a measure of maternal investment in reproduction and the extent of pre-parturition mortality. Given that fertility (litter size) will be dependent on the fecundity, it is important to have an understanding of the factors affecting fecundity, so that these can be applied to data from a given population.

Fecundity has been calculated for only a few scorpions (Smith 1966; Polis and Farley 1979); individual and intraspecific variability and the factors influencing this variability have not been studied. This paper examines the potential lifetime fecundity and the factors affecting annual fecundity in the burrowing scorpion *Urodacus armatus* Pocock. *U. armatus* is a burrowing species widely distributed over arid and semi-arid Australia with no apparent habitat restrictions in terms of soil type or vegetation. Scorpion activity, as measured by the number of active burrows, is greatest in the period March to May (= Fall) with a smaller peak from September to October (= Spring). Parturition starts in February and the second instars disperse from their natal burrows in March and April. The gestation period is about 11 months.

MATERIALS AND METHODS

The study site was Durokoppin Nature Reserve (1030 ha), 150 km northeast of Perth, Western Australia. The reserve had a mosaic of heath, shrub and woodland communities. *U. armatus*, a medium sized (total length 75 mm) burrowing species was found throughout the reserve, but was most abundant in woodland patches where there were 1000-3000/ha (Smith unpublished data).

Samples of pregnant female *U. armatus* were collected from two woodland patches in September and October of 1985 and 1986 and in one patch, a further sample was collected in March 1986, giving a total of 198 females. Females were collected by placing pitfall traps (plastic drinking cups) in front of the burrows. The traps were visited at sunrise in the following days and any scorpions were removed and kept cool until they were weighed to the nearest 0.01 g that evening. They were then killed by heat shock and preserved in 70% ethanol.

In the laboratory, the length of the carapace, right chela and tail were measured to the nearest 0.01 mm and the specimen dissected to expose the ovariuterus. Attached to the ovariuterus were three types of diverticula (Fig. 1) as described for *U. manicatus* (Thorell) (as *U. abruptus*, Smith 1966). Rudimentary diverticula [(RD), small finger-like projections with the ovum at the distal end, with three distinct size classes]; Embryonic diverticula [(ED), large projections

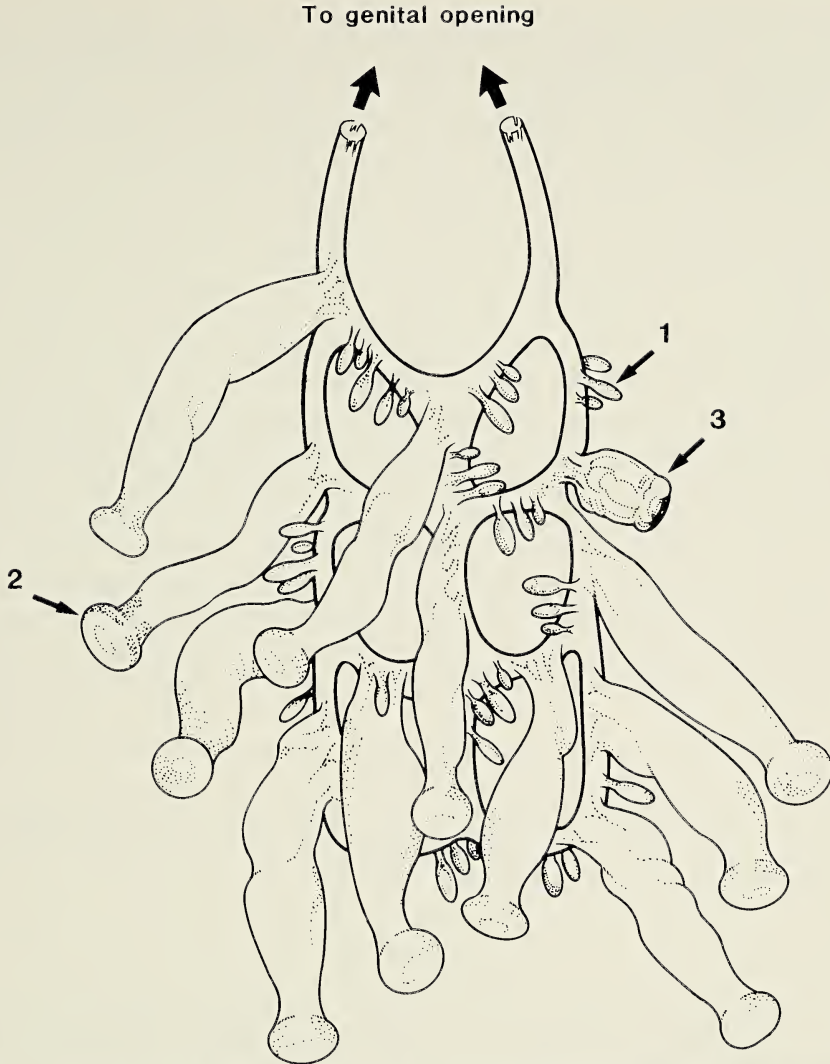


Figure 1.—Ventral view of the ovariuterus of *U. armatus* showing arrangement of Rudimentary diverticula (1) showing the three size classes, Embryonic diverticula (2) and one Post-Partum diverticulum (3) to indicate shape and size.

with a distinctive knob at the distal end and which contain the developing embryo] and Post Partum diverticula [(PPD, small, squat infolded structures that are formed from the sheath of the EDs when the young are born]. The numbers of each type of diverticula were counted and the length of the network of the ovariuterus (OUL) was measured to the nearest 0.1 mm from the first proximal bifurcation on the lateral branches. The numbers of *in utero* deaths (= abortions) in both the current and previous pregnancies were recorded. Abortions in the current pregnancy had EDs that were shorter and thinner while abortions from previous pregnancies were distinguished by the diverticula being very short, thin and dark.

The relative age of adult females was calculated from the formula: $\text{No. PPD} / \bar{XED} + 1$. Assuming that if the numbers of PPDs were equal to or less than the

maximum number of EDs (from all samples), then they represented the first pregnancy for that individual. Knowing the mean number and range of embryos in the first and second pregnancies, the relative age of females that had had more than two pregnancies was recalculated. This procedure was repeated a number of times to produce Table 1, which was used to assign age classes to individuals. Clearly, for the individual, the method was accurate only for females in their first and, to a lesser extent, in their second pregnancy. For later pregnancies, the accuracy was unknown, but for large samples, the errors should have cancelled out each other. In this scheme, relative age was related to the number of pregnancies; its relationship to chronological age was uncertain because not all females bred every year (the number of females that did not breed is indicated by the difference in the sample sizes for ED and CL in the first four samples in Table 3) and the age at maturity was not known with certainty. Log-log plots of carapace length against length of the right chela did not give distinct clumps but suggested that adults were in their sixth instar. Using the theoretical method of Francke and Sissom (1984) to calculate the number of molts between the second instar and the adults also suggested that adults were in their sixth instar (Smith unpublished data). Second instar *U. armatus* remained in that stadium for about 12 months and assuming that later stadia were of similar duration, then females mating after their final molt were in their fifth year. For convenience, relative age or number of pregnancies will be called simply age in the following discussion.

In analyzing the data, the length of the carapace was used as a measure of size (CL) and the condition (C) of the female was calculated from the formula $C = \sqrt[3]{\text{mass}/\text{CL}}$.

Females were collected in September and October to take advantage of the increased activity at this time and to ensure that the EDs had developed to a stage where they could not be confused with RDs.

RESULTS

Potential lifetime fecundity.—Examination of the samples from September and October showed that the ovariole in an immature female was a thin tube with no diverticula. In the fifth and possibly fourth instar, it had a number of small dense patches that may be sites of the developing ova and diverticula. By autumn, after the final molt, the ovariole was fully developed with RDs of three distinct size classes (Fig. 1). Presumably the ovariole of a fifth instar female finished its final development shortly before or at about the time of the final molt.

Initial inspection of the data suggested that a female's lifetime complement of ova were formed by the time she reached adult size, and that the sum of three types of diverticula were a measure of the potential lifetime fecundity, assuming that the PPDs were not resorbed.

This idea was tested with the present data in two ways. Firstly, in the March 1986 sample, the total number of diverticula in virgin females and those who were in their first pregnancy, should not differ significantly from those in their second or later pregnancies. The respective means, 51.7 and 55.5, were not significantly different ($t = 1.62$, $df = 23$, $P > 0.05$).

Secondly, the number of RDs should decline with age while the total number of diverticula (TD) should not differ significantly with age. The number of RDs

Table 1.—The calculated means of Embryonic diverticula (ED) and Post-Partum diverticula (PPD) with the range of PPDs for female *U. armatus* which have had 1 to 8 pregnancies.

No. pregnancies	Mean ED	Mean PPD	Range PPD
1	9	—	—
2	8	9	< 12
3	8	17	13-21
4	7	25	22-28
5	7	32	29-35
6	6	39	36-42
7	6	45	43-48
8	6	51	49-55

showed a steady decline from 44.5 at age one to 17.8 at age six (Table 2). One six year old had no RDs and the one seven and one eight year old had 20 and 8 RDs respectively. While the decrease from one age to another was less than expected from the number of embryos for different ages shown in Table 1, the true extent of the decline was masked by the variability in the numbers of TDs. A better indication of the progressive use of RDs with age was the mean percentage of TD that were still RDs (Table 2). This percentage fell from 82.6% at age one to 20.0% at age six which agreed well with the expected decline when it was calculated from the mean number of TDs and the annual fecundity with age given in Table 1 (Table 2).

The mean number of TD increased from 53.8 at age one to 62.7 for the combined five to eight age group (Table 2) and there was a significant difference with age (ANOVA $F = 6.38$, df 4, 186, $P < 0.01$). The mean number of TDs in the five to eight year olds was significantly greater than the mean TDs for one and two year olds, three and four year olds also had significantly larger mean TDs than one year olds (Newman-Keuls test, $P < 0.05$). The relationship between TD and the age, size (CL) and size of ovariole (OUL) of females was analyzed using multiple regression with a log transformation of the data from 186 females. Age had no significant effect on TD, while CL and OUL has significant positive effects, the variance ratios were 24.15 ($P < 0.001$) and 29.15 ($P < 0.001$) respectively. The relationship was expressed by the equation:

$$\log TD = 2.651 + 0.01282 CL + 0.001517 OUL.$$

Table 2.—Mean and standard deviation (SD) at different ages of the number of rudimentary diverticula (RD), the mean percentage of RDs ($RD \times 100/TD$), the calculated percentage of RDs (Calc % RD) using the average number of diverticula and the age related fecundity (Table 1) and the mean and standard deviation of the total number of diverticula (TD) in female *U. armatus*. * = mean and standard deviation from combined five to eight year old females.

Age	RD		RD \times 100/TD		Calc %RD	TD		Sample size
	Mean	SD	Mean	SD		Mean	SD	
1	44.5	6.9	82.6	3.2	84	53.8	7.4	68
2	39.0	6.5	68.8	5.0	70	56.2	9.4	51
3	34.7	6.8	57.5	5.4	56	59.5	8.0	40
4	26.5	4.9	44.4	4.0	44	59.1	5.0	21
5	20.5	8.9	57.5	12.3	32	62.7*	6.7*	7
6	17.8	9.0	20.0	15.7	21			5
7	20	—	—	—	11			2
8	8	—	—	—	0			1

These data show that the increase in TDs with age was related to the increase in CL and OUL with age (survivorship increases with size) rather than the development of new RDs.

Annual fecundity.—The mean, standard deviation and range for fecundity and five factors that may affect fecundity are given for each sample in Table 3.

Overall annual fecundity ranged from 4 to 12 with a mean of 8. Initial inspection of the above factors suggested that all exerted some effect. The data were then analyzed using an analysis of covariance with a log transformation using the GLIM program (Baker and Nelder 1977). In the sample of 198, the data from 29 females which were not pregnant were deleted for the first analysis. The analysis showed no significant difference between the samples (variance ratios from -0.3883 to 2.127) and the data from the samples were combined. The effect of four factors (Carapace length, age, condition and TD) on fecundity were then analyzed. TD, with a variance ratio of 0.8367 , was insignificant and was dropped. Condition, with a variance ratio of 2.239 , also not significant, was dropped, leaving age and size as the only significant factors with variance ratios of 6.407 and 5.455 respectively. The analysis was repeated with ovariole length (OUL) but excluding TD and excluding 11 females for whom data of ovariole length were not available. OUL was not significant (variance ratio 0.5191), leaving age and size again as the only significant factors affecting fecundity with variance ratios of 7.125 and 5.068 respectively.

The simplest adequate model explaining variation in fecundity was given by the formula:

$$\log ED = 0.9656 - 0.07003 \text{ Age} + 0.01839 \text{ CL}$$

The realized reproductive potential or the number of live births (fertility) is not necessarily the same as the fecundity because of the possibility of abortions. Of the 198 females examined, 70 had had abortions; only 4 of these were in EDs (1, 2, 2, 3). This suggested that most abortions that were recognized were in the latter half of the gestation period. Overall, the mean number of abortions per pregnancy was 0.8. In 17 age-two females, 12 had only one abortion, 3 had two abortions and one each had 5 and 6 abortions. Data from older females suggested that this was reasonable indication of the range of the numbers of abortions per pregnancy, based on the average number per pregnancy.

Number of pregnancies.—Females with the mean number of TDs and average fecundity (Table 1) could have eight pregnancies, however, females with TDs at the extremes of the range (34 to 80) could have from 5 to 12 pregnancies. Examination of the number of RDs in 4, 5 and 6 year old females showed that the potential number of pregnancies that they could have ranged from 7 to 11, 7 to 11 and 6 to 10 respectively. The two 7-year olds could have had another three pregnancies while the one 8-year old could have had one more pregnancy. Clearly, few, if any females, survive long enough to realize their full reproductive potential.

DISCUSSION

The true measure of fecundity is the number of fertilized ova; however, this is not an easy measure to obtain and is probably not important in the population dynamics of *U. armatus* given the limited provisioning required at this stage of

Table 3.—Mean (\bar{X}), standard deviation (SD), range (rg) and sample size (N) of the number of embryonic diverticula (ED), total number of diverticula (TD), carapace length (CL), condition (C), Age (A) and length of ovariuterus (OUL) in female *U. armatus*. Note that sample sizes vary within a sample because some females were not pregnant or the data for some factors were not available.

Sample		ED	TD	CL	C	A	OUL
Area 1 1985	\bar{X}	7.7	58.8	6.87	0.145	2.7	321.9
	SD	1.67	9.22	0.34	0.006	1.40	38.11
	rg	4-12	44-80	6.2-7.4	0.128-0.157	1-8	249-434
	N	50	53	53	53	53	50
Area 1 1986	\bar{X}	8.8	54.9	7.05	0.145	2.2	306.2
	SD	1.86	8.20	0.35	0.008	1.46	32.46
	rg	4-12	34-76	6.4-7.7	0.122-0.167	1-7	248-390
	N	58	59	63	63	63	57
Area 2 1985	\bar{X}	8.7	59.6	7.43	0.141	2.3	327.3
	SD	1.73	6.76	0.29	0.006	1.34	50.82
	rg	5-11	40-71	6.9-8.1	0.120-0.152	1-7	267-430
	N	20	24	24	24	24	23
Area 2 1986	\bar{X}	8.4	57.2	7.08	0.142	2.6	303.7
	SD	1.25	7.33	0.38	0.008	1.41	32.20
	rg	6-11	45-72	6.1-7.9	0.111-0.157	1-6	249-364
	N	30	32	32	32	32	30
Area 2 March 1986	\bar{X}	8.3	53.8	7.17	—	2.2	286.3
	SD	1.34	6.39	0.39	—	1.35	22.55
	rg	6-11	47-65	6.5-8.1	—	1-6	250-350
	N	15	25	26	—	26	262

development. Fecundity in this study was calculated at about halfway through the gestation period and was not significantly different from that obtained shortly after mating. It is therefore the best time to collect samples as it takes advantage of the increased activity and avoids any confusion in the identification of RDs and EDs. Further, the data suggest that most abortions probably occur in the second half of the gestation period.

Mean fecundity for the study was 8.3, which was considerably smaller than the mean fertility of 31.3 calculated by Polis and Farley (1979) from data on 39 species. More recently, Polis and Sissom (1990) have provided data from 77 species on litter sizes, which ranged from one to 105, with a mean of 25; only 11 species had litter sizes comparable to the fecundity of *U. armatus*. The data were not detailed enough to make statistical comparisons, however, from the data available it is clear that fecundity in *U. armatus* and its variability (CV for the 5 samples range from 14.9% to 21.8%) is among the lowest found in scorpions.

The only comparable study is that of Smith (1966), who calculated that fecundity in *U. manicatus* (a slightly smaller species, CL = 5.7 mm) to be 15.7 with 4.5% of embryos being aborted. The litter size of females in the field was 11.4, indicating a 24% mortality in immediate post-birth period.

The factors influencing variation in fecundity were examined; size had a significant positive effect while age had a significance negative effect. Other factors (condition, length of ovariuterus and total number of diverticula) had positive but not significant effects. Size and age affect intraspecific fecundity in

both invertebrates (see Introduction for references) and vertebrates (Allaine et al. 1987; Sauer and Slade 1987). In invertebrates, size is commonly a positive factor, but in some species or situations, it may be neutral or negative in its effect (Haack et al. 1987). Similar effects are seen in relation to age (Davies 1987; Ribi and Gebhardt 1986). Francke (1981) showed that female size (CL) and the size of second instar young (CL) accounted for 81% of the variability in litter size in an interspecific study of diplocentrid scorpions. Bradley (1984) found that adult size (CL) in *Paruroctonus utahensis* Williams was not related to brood size (second instar) or the weight of the young. There are no data on the relationships between fecundity and size of young in *U. armatus*, however in *U. manicatus* there was no significant relationship between female size (CL) and the size (CL) of either first or second instars (Smith, unpublished data).

Female condition reflects the amount of food stored in the hepato-pancreatic gland and indirectly, the females foraging efficiency and/or success. For most females collected in spring, just after reopening their burrows, condition should reflect the foraging success in autumn at mating and it might be expected that variations in condition would be reflected in the fecundity as is found in other arachnids (Wise 1975). The lack of a significant effect is similar to Bradley's (1984) finding that feeding rates do not effect brood size nor the size of the young (second instars) in *P. utahensis*. Also, Polis (1988) found that in *P. mesaensis* Stahnke, high levels of food intake increased the rate of development but not the fecundity. On the other hand, starvation eventually led to the resorption of the embryos. Similar observations have been made on various *Urodacus* species (Smith, unpublished data). Metabolic rates in scorpions are very low (Hadley and Hill 1969; Riddle 1978) and it is likely that energy requirements for the embryonic development in the first half of the gestation period are also low. If the energy requirements of pregnant female *U. armatus* are similar to those of *P. utahensis* and *P. mesaensis*, then food would not be a limiting factor for *U. armatus*, except under the most severe conditions. Under average conditions, reproductive potential is strongly influenced by the size and age of the population. Size itself may be influenced also by the individual's rate of development.

Studies on female lifetime reproductive success in invertebrates appear to be limited to a few studies on Odonata (Fincke 1987; Banks and Thompson 1987; Koenig and Albano 1987) and the monarch butterfly (Svård and Wiklund 1988) and are not comparable with a viviparous iteroparous invertebrate, with determinate lifetime fecundity. Perhaps a better comparison is with mammals, where oogenesis and follicular formation is completed at about parturition. However, in mammals, the number of follicles far exceeds those required even under the most favorable breeding conditions (Gosden and Telfer 1987).

In this study, I have used morphological characteristics of the ovariole and its diverticula to demonstrate that all the ova are developed and enclosed in rudimentary diverticula around the time the female molts into her last instar and that the ova are progressively used over the lifetime of the female. A study of *U. manicatus* showed a similar relationship between the numbers of the different types of diverticula with age. Further, limited histological examination of the ovariole of females of different age showed no evidence of new ova being developed after the females had completed their final molt. Examination of a limited number (1-20) of 5 other species of *Urodacus* suggests that all *Urodacus*

may have a similar reproductive strategy and further, that this strategy may be common to all scorpions with katoikogenic development (Scorpionidae and Diplocentridae).

The reproductive strategy of *U. armatus* is one of long life, delayed maturity and low potential lifetime fecundity and annual fecundity; traits that have probably coevolved with the habit of burrowing and foraging from the burrow entrance; both will increase survivorship. The most vulnerable period for *U. armatus* is when the second instar individuals are dispersing from their natal burrows as was found for *U. manicatus* (Smith 1966). Once the second instars have dug their own burrows, survivorship is probably high and hence there is no need for a high reproductive rate. These adaptations are characteristic of equilibrium species and are typical of a number of scorpion species that create their own stable and predictable environment by constructing burrows (Polis and Farley 1980). Further these adaptations may be viewed as a refinement of those that led to the development of the extremely low metabolic rate which appear to be characteristic of all scorpions (Polis 1988).

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COURTSHIP AND MATING BEHAVIOR OF *THELECHORIS KARSCHI* (ARANEAE, DIPLURIDAE), AN AFRICAN FUNNELWEB SPIDER

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ABSTRACT

The courtship of *Thelechoris karschi*, an African funnelweb mygalomorph spider, consists of an early non-contact phase of vibratory signaling and then a contact phase involving leg-fencing and, sometimes, lunging. Eventually the male clasps the female's pedipalps with his first tibial apophyses, tilts her upwards and backwards, and attempts to insert his palpal organs alternately. There was much variation among successful courtships in the amount of aggression (lunging and chasing). Mating was characterized by numerous bouts of unsuccessful palpal insertion attempts, relatively few successful insertions, and a tendency for repeated courtships and copulations. It is pointed out that ample opportunity for sexual selection by female choice exists during these courtships and copulation attempts, and that the lengthy and repeated copulations may be, in part, a consequence of genital anatomy.

INTRODUCTION

Thelechoris karschi Bösenberg and Lenz is a moderately large diplurid spider (adult body length 11-20 cm) with extremely long lateral spinnerets which are used to build conspicuous, perennial capture webs. The webs consist of a large (up to 1500 cm² viewed from above), three-dimensional, exposed capture area of interconnected sheets and passageways funneling into a protected tubular silk retreat, and are located in a wide variety of microhabitats, from rock piles and road banks to tree trunks and shrubs. This species is quite common in some localities and occurs in a wide variety of arid to mesic habitats (except for extreme habitats like desert and wet forest) over a large part of eastern and south-central Africa, from Kenya southwest to Namibia.

Of the 18 currently recognized genera of Dipluridae (Raven 1985; Coyle 1986a), observations of courtship and/or mating have been published for only four: *Microhexura* (Coyle 1985), *Euagrus* (Coyle 1986b), *Australothele* (Raven 1988), and *Phyxioschema* (Raven and Schwendinger 1989). The observations presented herein on the courtship and mating of *Thelechoris karschi* are the first for this genus and its subfamily (Ischnothelinae). A similar study of reproductive behavior in the other two ischnotheline genera (*Ischnothele* and *Lathrothele*) is currently being conducted by the first author.

Our primary objective in this study was to carefully describe the courtship and mating behavior of *T. karschi* to obtain behavioral characters for eventual use in

testing phylogenies. Secondary objectives were 1) to begin testing the hypothesis that the *T. karschi* populations we have been studying are not behaviorally isolated from one another and 2) to propose hypotheses about the functional significance and origins of some of the behaviors observed. We hope this paper will be a stimulus and a useful foundation for future studies.

MATERIALS AND METHODS

Although the spiders used in this study were collected from the following eight localities in three different areas of East Africa, a preliminary analysis of morphological variation suggests that they all belong to one species, *T. karschi*. The four populations (A-D) from the coast of eastern Kenya are about 130 miles east of population E in Tsavo West National Park in the interior of Kenya. Both of these sets of populations are about 900 miles north of the three populations (F-H) in southern Malawi.

Coastal Kenya: population A - Kilifi and 9 km N Kilifi, 10-50 m elev., old field with scattered trees, shrubs, and hedgerow, 27-29 March 1989; population B - Jimba, 3 km SE Gedi, 100 m elev., second growth forest, 28 March 1989; population C - Shimba Hills Natural Reserve, S Kwale, 330 m elev., camping area in forest patch, 31 March 1989; population D - Shelly Beach Road, few km S Mombasa, 30 m elev., old field with scattered trees, 1 April 1989. Interior Kenya: population E - Tsavo West National Park, Kitani Lodge, 41 km S Mitito Andei, 750 m elev., rock garden, 15 April 1989. Malawi: population F - along Likhubula River at base of Mulanje Mountain, 750-850 m elev., 18 April 1989; population G - 24-26 km N Zomba on route M1, 750 m elev., road bank, 21-22 April 1989; population H - Blantyre, 1000 m elev., yard and garden, 22 April 1989.

In the laboratory each adult male was kept in a clear plastic drinking cup covered with a petri dish lid and nested in an identical cup. A pad of moist cotton between the bottoms of the two cups provided moisture through a hole punched in the bottom of the inner cup. The 17 females used in the study were large (therefore presumably mature) and were active silk-spinners. Each of these constructed a web in an observation arena. One type of arena was a clear plastic shoe box ($29 \times 15 \times 8.5$ cm high) with construction paper covering its floor. Either a clear vial was taped to the floor at one end to serve as a retreat or the female was allowed to construct her retreat and capture web in any part of the arena. These webs were misted with water every other day. The other type of arena, resembling an "ant farm" container, allowed for especially close observation of courtship and mating without unduly restricting the participants. It consisted of two panes of glass (15×24 cm) separated by a 1.5-3.0 cm thick U-shaped wooden frame mounted upright on a wooden base. The female constructed her web between the panes of glass, a piece of styrofoam plugged the opening at the top of the frame, and water was periodically added to a wet cotton ball in the bottom of the arena. The spiders were maintained at 24°C and a 12-hour photoperiod. They were fed a mealworm (*Tenebrio*) larva approximately once every ten days, and rarely a cricket nymph or a few house flies.

Male-female encounters were initiated by gently dropping the male onto the female web far from her retreat. All encounters occurred between 6 May and 30 June (39 encounters) and 19 and 27 September (six encounters) 1989 during the

daylight period (primarily afternoon hours). Most encounters were recorded with a Panasonic WV-D5000 video recorder equipped with a Micro-Nikkor 55 mm close-up lens. The arenas were lighted from above by fluorescent ceiling lights and a fluorescent desk lamp and sometimes also from the front by a 75 watt incandescent bulb. Actions that were not being recorded through the lens were often recorded verbally on the audio channel of the recorder. Behaviors were analyzed with slow-motion and single frame advance modes (which allowed one second of action to be subdivided into 30 individual stop-action frames).

The spermathecae of 15 *T. karschi* females from several localities in East Africa were removed, cleared in 85% lactic acid, and examined and measured with a compound light microscope at 40X and 100X. The location of sperm and semen (recognized by their granular translucence) was recorded. Some spermathecae were drawn with the aid of a drawing tube. The palpal emboli of twelve males from the same localities were measured at 100X with a stereomicroscope.

RESULTS

Adult males were moderately common in populations A and C when sampled in late March, just before the onset of the rainy season (late March through May), and were very common (although still seemingly much less abundant than adult females) in population E in mid April, during the rainy season. No adult males were found in populations F, G, and H when they were sampled in late April, after the end of the rainy season (November to April) in southern Malawi. While some adult males were apparently in their own webs, others were in webs with females.

Table 1 summarizes outcomes of the 45 male-female encounters. Ninety percent of all courtships were initiated by the male. Eight of the 16 unsuccessful courtships (those that failed to progress to a copulation attempt) involved non-receptive females which did not perform any courtship signals, one involved an apparently unreceptive male that was briefly courted by the female, and the other seven involved reciprocal courting. In eight of the 14 encounters that led to copulation attempts (A, A, or X in Table 1) (a copulation attempt was defined as all the palpal insertion attempts occurring between the onset of clasping and the subsequent uncoupling event) there were multiple attempts, giving a total of 28 copulation attempts (and thus 28 "successful" courtships) during this study. Only two of the 13 encounters among spiders from coastal Kenyan populations led to mutual courtship, and neither of these led to a copulation attempt. Five of the 14 encounters initiated among population E spiders resulted in successful copulations (X in Table 1) (a copulation was judged successful if at any time the embolus was observed to be fully inserted and palpal flexions moved the female's abdomen; no additional effort was made to determine whether insemination actually occurred). Six successful copulations occurred between individuals from distant populations. Females E11 and E28 and males E3 and E6 each copulated successfully with more than one individual.

Since we have little or no information about the reproductive history of the 21 females used in this study, and since at least some of them had mated before they were collected (four that did not attempt copulation deposited fertile eggs), correlations between observed reproductive success and observed mating behavior are meaningless.

Table 1.—Outcomes of laboratory encounters of male and female *Thelechoris karschi*. Specimen code letters identify populations as described in Methods section. Outcomes indicated by following symbols: O = no courtship behavior; M = male courts briefly; F = female courts briefly; MF = both individuals court, but do not attempt copulation; A = copulation attempted (palpal insertions attempted), but no palpal insertions (A) or uncertain whether insertions occurred (A); X = copulation with palpal insertions. Multiple A's and/or X's indicate multiple copulation attempts in a single encounter. Repeat encounters of same individuals are separated by commas. Asterisks designate encounters that were ended by female attacks.

	MALES												
	Coastal Kenya						Interior Kenya						
	A1	A2	A3	A4	C1	C2	D1	E1	E2	E3	E4	E5	E6
FEMALES													
Coastal Kenya													
A20		M	M*										
A21	M,O	M,M											
B10	O								X,O				
B12	O	O,O	MF										
C12		MF											
D11										O			X
D12					O								
Interior Kenya													
E11										X	O*	XAAA	XA,AXXA
E17													XAAA*
E25									MF*	O			
E27							X						
E28		XA				XX							
E29								M*	O		MF*		O*
E30													
E31									F				O
Malawi													
F10		A											
F11			M*										
F14										O	MF		
G11										X	MF		
H10										AA*,M*		AA	
H11				MF		O							

Ten (22%) of the encounters were ended by clearly life-threatening attacks by the female (Table 1). Five of these were interrupted early (we removed the male before he was injured) and five (that were not interrupted as quickly) resulted in serious injury to the male, i.e., severed legs (three attacks), a broken leg (one attack), and a severed spinneret (one attack). Six of the attacks occurred early in the encounter, either before any courtship behavior (two attacks) or while the male was courting non-courting females (four attacks). Although three of the other four attacks occurred either after a failed attempt at clasping (one attack) or after copulation attempts (two attacks), none occurred immediately after uncoupling; the fourth attack occurred several minutes after uncoupling as the male moved about the web in the confines of the observation arena.

Behavioral units.—The following section describes each of the behavioral units which collectively comprise *T. karschi* courtship and mating behavior.

Advance: forward movement which brings one spider closer to the other. Often an advance is an ambulatory advance involving the displacement of all tarsi, but some advances consist only of a shifting forward of the anterior legs or body. Advances may be accompanied by other behavioral units (quivering, twitching, jerking, and tapping). Lunges and chases are special aggressive advances.

Lunge: sudden vigorous forward and/or downward thrust of the body toward the other spider with the chelicerae spread apart and the fangs extended. The lunges are stereotyped; they appear to be ritualized attacks which stop short of their target or are sometimes directed slightly to one side of the target. Only one lunging about (E3 \times E11) escalated into what approximated a real fight, but neither spider was injured and the courtship eventually culminated in a successful copulation.

Chase: very rapid pursuit of the other spider.

Retreat: movement which increases the distance between the spiders. It may involve backing away or turning away (which may then continue as forward movement).

Pause: interval between two actions when the spider is not moving. Pause postures are variable.

Quivering, twitching, and body jerking: vibration-generating appendage (and often body) movements which comprise a continuum. They are sometimes difficult to distinguish from one another and may occur together in the same bout. Twitching is one or a few distinctly separate sudden flexions or extensions of one or more legs and/or pedipalps. Quivering is high frequency, usually low amplitude, continuous twitching. Sometimes quivering involves only one or a few appendages, but usually all legs and appendages are moving simultaneously. Sometimes the entire body, especially the abdomen, quivers. Body jerking is a particularly high amplitude twitching of all legs and pedipalps so that the entire body jerks one or more times in succession. Female body jerking may visibly vibrate the web and the male, even if he is several body lengths from the female.

Bouts which combine quivering, twitching, and even body jerking are common. A courting male often begins low amplitude twitching which gradually increases in frequency and amplitude to become a high amplitude quivering (or rapid twitching). Sometimes a female's legs quiver as she slowly flexes them and then twitch as they are suddenly relaxed and reextended. At other times all her legs and pedipalps twitch simultaneously and then quiver for a while. Sometimes a female whose pedipalps and anterior legs are twitching or quivering will suddenly

shift to body jerking. Often the pedipalps and first legs appear to quiver or twitch with greater amplitude than other appendages. Although quivering, twitching, and body jerking are usually performed when the spider is not advancing, sometimes a female will jerk-walk, jerking and quivering her appendages and body while she walks through the web. Although most quivering, twitching, or body jerking lasts for less than 1 or 2 s, occasionally a bout lasts longer; one especially long bout (48 s) of virtually continuous quivering and body jerking was performed by a female (H10) just before the final leg-fencing bout leading to clasping.

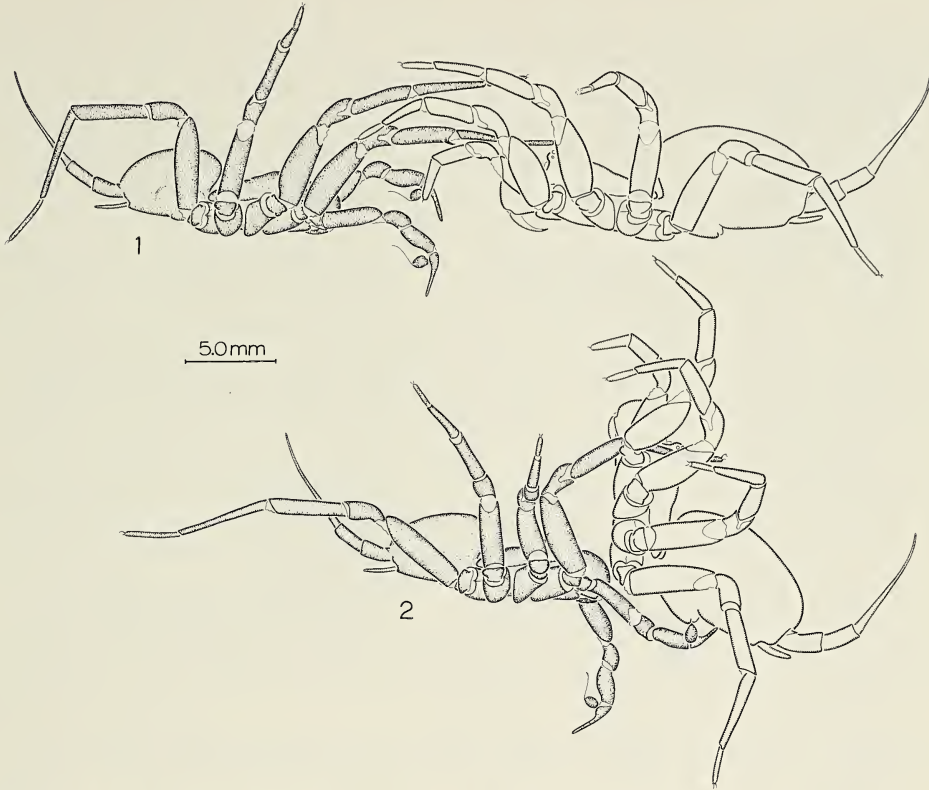
Tapping: repeated, rather rapid, non-synchronous lifting and lowering of the pedipalps and first legs so that they contact the web forcefully. Tapping often occurs just prior to or during advances and silk-walking. Sometimes tapping is combined with quivering, or alternates with quivering or twitching bouts, or occurs alone in the same behavioral context.

Silk-walking: jerky stop-and-go walk performed by the female during which she periodically applies silk to the web. Silk-walking is often performed directly in front of the male, and may continue all the way back to, and inside, her retreat. Males were observed to briefly spin silk while courting only two times during this study.

Leg-fencing: semi-stereotyped sparring of the male with the female. The spiders face one another and lower and raise and flex and extend their first and second legs and pedipalps so that each spider's appendages overlap, move past, and brush against those of the other spider (Fig. 1). During leg-fencing the body is often raised and lowered and the fangs are sometimes extended. The female usually flexes her fencing appendages further, moves them more rapidly, and is more likely to extend her fangs than is the male. The male's legs tend to be more extended and stiffer than those of the female; in general his movements appear less aggressive and more protective than hers. Lunges sometimes occur during leg-fencing. As a fencing bout proceeds, the male's first legs may extend more fully and decrease their movement as they prepare to slide into the clasping position. During fencing the male usually raises and forcibly lowers his pedipalps (more or less alternately) so that the cymbial apophyses punch down into the web. The duration of leg-fencing bouts is quite variable (Table 2), but they usually last less than 6 s.

Clasping: The clasping process begins during leg-fencing as the male gradually raises, extends, and stiffens his first legs. He then advances a little to place each of them between the nearest chelicera and pedipalp of the female. The mating apophysis at the end of the male's first tibia (Fig. 1) engages the base of the female pedipalp prolaterally, presumably at either the trochanter or the coxal endite (we were not able to observe the exact point of engagement). After the claspers are engaged, the male continues advancing and tilts the female's cephalothorax up and back. During the clasping process, the male continues the pedipalp tapping; drumming that commenced during leg-fencing.

Palpal insertion attempts: Shortly after the clasping male has advanced so that his chelicerae are nearly touching the female's fourth leg coxae, he begins a series of palpal insertion attempts. One pedipalp is lifted into position, fully extended, and rotated (primarily at the coxa-trochanter joint) 100-120° (clockwise for the left and counterclockwise for the right pedipalp) to position the palpal organ above and ectal to the cymbium and close to the female's genital opening (Fig. 2).



Figures 1-2.—Courtship and mating behavior of *Thelechoris karschi*; side view, drawn from video tape and preserved specimens; male dark, female light. Only appendages on near side are illustrated, except for male's left pedipalp. 1, leg-fencing. 2, copulation.

The other pedipalp is held semi-extended below the male. Periodic flexions of the distal three joints of the active pedipalp lift the tibia and tarsus. These and synchronous lateral movements at the patella-tibia joint and 90° twisting movements of the palpal organ at its junction with the cymbium generate probing thrusts (typically about one per s) of the long embolus close to the female's genital opening. A palpal insertion attempt bout consists of a series of these thrusts which are sometimes interrupted by pauses. At the end of a bout the active pedipalp is lowered to the resting position below the male and the other pedipalp is lifted and a new bout of insertion attempts begins.

The following posture characteristics were consistently observed during these palpal insertion attempts (Fig. 2): 1) The male's chelicerae were touching or almost touching the female's fourth coxae. 2) The angle between the male and female cephalothoraxes was 80-100°. 3) The female's pedicel was flexed upwards so that the cephalothorax-abdomen angle was 40-80°. 4) The male's first legs were bent approximately 90° at the femur-patella joint and the distal (clasping) end of each tibia was against the prolateral surface of each female pedipalp base. 5) The female appeared to be cataleptic (motionless with legs and pedipalps partly flexed) except for occasional quivering or other movements. During some copulation attempts it was possible to see that the female's genital area was distended and the anterior and posterior genital lips were protruding and parted so that the genital opening was more exposed than usual. The male's second legs

Table 2.—Data for the 21 *Thelechoris karschi* courtships and copulation attempts that were video recorded. In the "palp insert" column, N means no palpal insertions, Y means at least one insertion bout, and a question mark indicates that we could not be certain whether an insertion occurred. In the "duration" column, "A" is the time from the first courtship behavior to the onset of leg-fencing, "B" is the time from onset of first leg-fencing to clasping, and "C" is the duration of the copulation attempt (from clasping to uncoupling). Range, mean, and standard deviation given for leg-fencing durations. The number of lunges by the male ("M") and the female ("F") are given in the "lunges" column. The "uncouple" column indicates which individual appeared to actively uncouple. Question mark in the leg-fencing or lunges columns indicates that segments of these courtships, and therefore some of these actions, may not have been recorded.

Spiders	Date	Palp insert	Duration (min)			Leg-fencing			Lunges		
			A	B	C	Bouts	Duration (s)		M	F	Uncouple
E3×H10	5/15	N?	5.00	6.30	4.95 11.38	4	3-18 (8.0 ± 6.8)		15	10	M
E6×E17	5/15	N?									F
		Y	27.10	3.45	6.67	7?	1-10 (6.4 ± 3.1)		7?	12?	MF
		?	0.07	16.78	3.40	13?	1-18 (4.0 ± 4.6)		15?	22?	M
		?			<2.00						
		?			6.03						M
A2×F10	5/17	?	30.92	0.10	~26.00	1	6		2	1	
E2×B10	5/17	Y			31.10						M
E6×E11	5/19	Y	9.57	13.18	17.72	17	1-20 (6.9 ± 6.5)		12	36	F
		N	0.05	1.68	0.47	3	5-6 (5.3 ± 0.6)		1	0	M
E6×D11	5/23	Y			14.08	3	4-12 (6.7 ± 4.6)		0	0	M
E3×E11	5/23	Y	7.83	46.57	90.73	10	1-47 (16.3 ± 14.1)		10	18	F
E6×E11	5/30	N	0.30	0.97	1.08	3	1-25 (11.0 ± 12.5)		5	6	F
		N	0.08	0.32	5.00	1	9		0	0	F
		Y	0.02	0.53	14.32	2	5,19		0	0	F
		N	3.50	1.32	5.03	2	1,12		0	0	M
		Y	19.83	0.17	39.67	1	10		0	0	M
E3×G11	6/7	Y	0.47	7.00	108.85	2	9,45		0	0	F
E5×E11	6/13	?	0.02	3.52	4.47	5	7-28 (18.4 ± 7.9)		0	0	F
		?	0.13	0.28	1.30	1	17		0	0	F
		N?	0.55	0.15	1.55	1	9		0	0	F

were either extending upward and outward against the web or upward and forward to lightly contact the female's first or second legs. Male legs III and IV were usually extended (pushing) backwards and outwards against the web. If the spiders were suspended in the web (probably the normal situation), the male's cephalothorax was horizontal or inclined slightly downward and his abdomen was on nearly the same plane. However, if the pair was on solid substrate, the male was typically under the front of the female with his cephalothorax inclined upward at an angle of 35-75° and his abdomen nearly horizontal. During one apparently unsuccessful copulation, the pair maintained this posture (relative to one another) while gradually rotating 110° onto their sides.

A successful insertion bout begins with the insertion attempt movements described above. Then, as the embolus tip enters the genital opening, these earlier movements stop and the three distal palpal joints flex to insert the entire length of the embolus into the opening (Fig. 2). Occasionally the palpus is held motionless in this inserted position for awhile, but more commonly the pedipalp performs repeated pulsing flexions (of the distal joints), each of which visibly pulls and twists the female's abdomen toward the male. During this series of alternate flexions and extensions, the embolus is never withdrawn from the genital opening, indeed its sliding movement within the female genitalia appears minimal. One such series of 20 flexions by an inserted palp lasted 38 s. Another much longer series (274 s) of slower and less regular palpal flexions involved one flexion every 2-5 s.

Uncoupling: pulling away of one spider from the other to end the copulation attempt.

Figure 3 summarizes our observations on the sequence of both male and female behaviors during courtship and mating in *T. karschi*. The courtship and mating process can be divided into two phases. Phase I includes non-contact behaviors and phase II includes behaviors which involve contact (or virtual contact) between male and female. Transition from phase I to phase II necessitates an advance into contact. Retreats and chases are transitional behaviors that shift the courtship from phase II back to phase I.

Male activity in phase I is primarily cyclic, i.e., a series of short advances, or quivers then advances, or quivers, with each action separated by a pause of highly variable duration. This cycle of male activity ends when contact with the female leads to leg-fencing and/or lunges (phase II behaviors). Re-entry to this cycle may occur after retreats from contact courtship (phase II). Often, female behaviors (quivers, silk-walking, advances) follow the retreats and appear to trigger a new cycle of male non-contact signaling.

Ninety percent of the time that the spiders advance into contact from phase I behavior, leg-fencing or lunges occur. Sooner or later these phase II behaviors usually lead to retreats back to phase I courtship; only 23% of the leg-fencing bouts we observed led directly to clasping. The number of leg-fencing bouts performed before a courtship proceeded to clasping varied from 1 to 17 (Table 2).

From courtship to courtship, there is much variation in the amount of lunging. Both male and female lunging were common in only 6 of the 17 courtships for which we have complete video records of contact courtship (Table 2). None of the spiders (E3, E6, E11) that mated with more than one mate were consistently aggressive or non-aggressive in all courtships. In two (E6 \times E11) of the three encounters with a sequential series of multiple courtships and matings for which

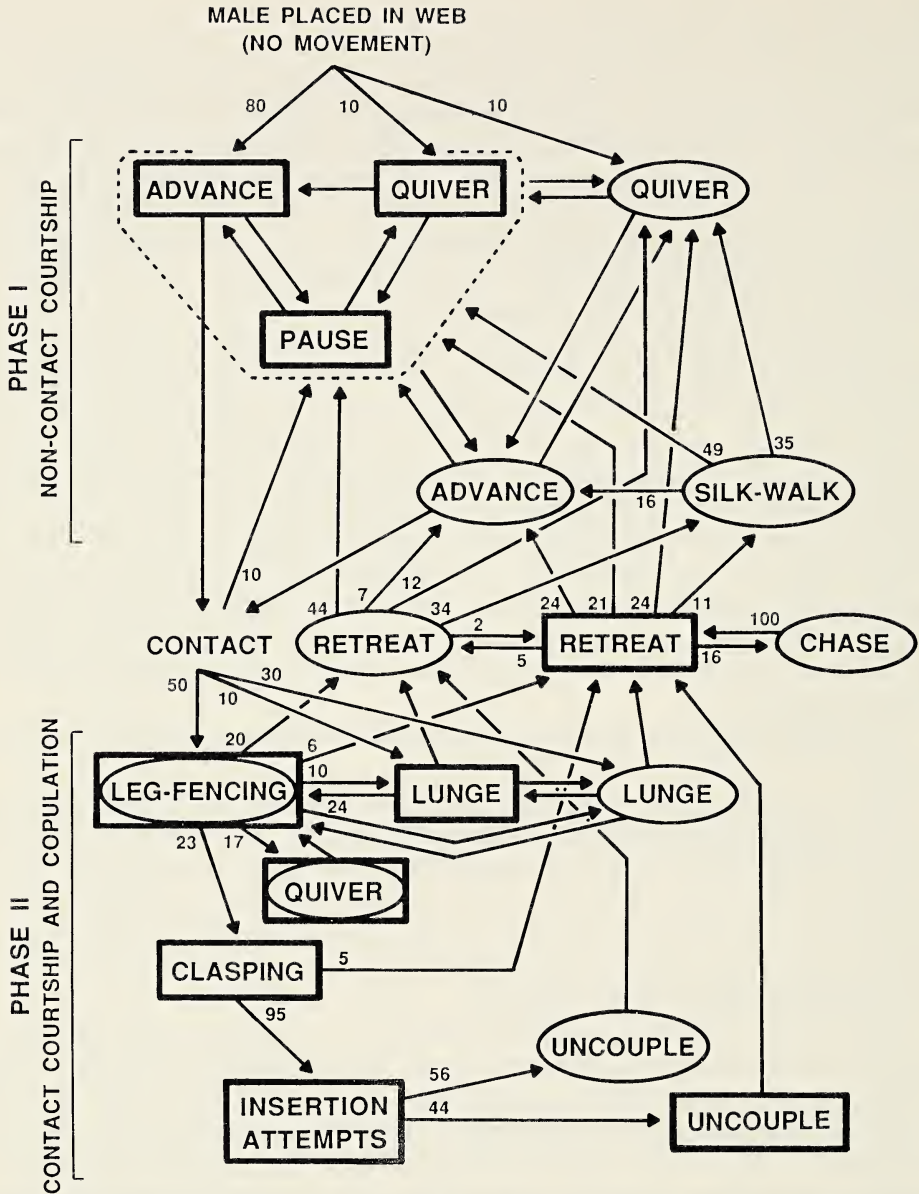


Figure 3.—Summary of the sequence of *Thelechoris karschi* courtship and mating behaviors, based on an analysis of the 21 courtships and copulation attempts recorded on video tape. Male behaviors in boxes; female behaviors in ellipses. Arrows indicate sequence and numbers indicate the percentage of times a particular behavioral unit is followed by another. Quiver boxes and ellipses represent not only quivering, but also related behavioral units commonly associated with quivering, i.e., twitching, body jerking, and some forms of tapping. Although both male and female frequently pause during courtship and mating, only the male pauses which occur repeatedly during the non-contact phase of courtship are included in this diagram.

we have complete video records, there was a drastic decrease in lunges after the first courtship of each series; the other such encounter (E5 \times E11) involved no lunging. The courtship lunging of female E11, which mated successfully on four different days during a four-week period, decreased gradually and drastically during that period.

Overall, we observed 105 female and 67 male lunges. In four of the six courtships with many lunges, females lunged considerably more often than males. The amount of lunging tends to be correlated with the amount of leg-fencing, which is a consequence of the fact that lunges tend to precede, follow, and/or be nested within leg-fencing bouts. A higher proportion of female lunges (71%) than male lunges (37%) were nested in leg-fencing; females lunged 3.2 times more often than males during leg-fencing. The male lunge box and female lunge ellipse in Fig. 3 represent individual lunges or bouts of repeated lunges that were not nested within a leg-fencing bout. Although lunges are sometimes followed by full retreats from contact courtship, most lunges are followed by other lunges or leg-fencing; these lunges usually cause the other spider to momentarily reel backward, but we did not count this as a retreat since the spider rebounds instantly. Sometimes lunging was reciprocal; sometimes it was not, with two or more female lunges (common) or two or more male lunges (less common) in succession. Chasing, which occurred only in courtships with much lunging, was performed only by females.

The transition from leg-fencing to clasping to palpal insertion attempts occurs rather quickly. The clasper positioning process lasts from 2 to 15 s (mean = 5.4, SD = 2.9 N = 17) and the period between the completion of clasper attachment and the first palpal insertion attempt lasts from 1 to 30 s (mean = 6.8, SD = 6.7, N = 16). Following the onset of clasping, female leg-fencing rapidly decelerates and shifts to quivering so that by the first palpal insertion attempts, she exhibits the typical cataleptic copulatory posture (Fig. 2). The only time this did not occur was when a male (E6) was clasping the female (E17) abnormally (with only his left first leg); she extended her fangs and pushed him away while he was reaching with his pedipalps to initiate insertion attempts.

The recorded courtships and copulation attempts varied widely in duration (Table 2). Successful copulations were significantly longer (N = 8, range = 6.67–108.85 min, mean = 40.39, SD = 38.4) than the clearly unsuccessful copulation attempts (N = 4, range = 0.47–5.03 min, mean = 2.90, SD = 2.5) and the copulation attempts of questionable success (N = 9, range = 1.30–26.00 min, mean = 6.79, SD = 7.8) (P < 0.01, Mann-Whitney U).

Unsuccessful copulation attempts consisted of a series of unsuccessful palpal insertion attempt bouts and occasional pauses within bouts or between bouts when neither pedipalp was moving (usually both pedipalps were lowered). Even within one copulation attempt, these insertion attempt bouts varied considerably in duration. For example, in one apparently unsuccessful copulation attempt (E3 \times H10) there were 22 bouts of unsuccessful insertion attempts and these bouts ranged from 2 to 34 s (mean = 10.5, SD = 7.4) in duration.

Successful copulations involved bouts of unsuccessful palpal insertion attempts and one or more bouts with successful insertions. These successful insertion bouts did not occur at the beginning of a copulation, and were more common during the second half than during the first half of a copulation attempt. Successful insertion bouts typically lasted longer (range = 58–277 s, mean = 111.8, SD =

68.0, $N = 13$) than unsuccessful bouts (range = 2-87 s, mean = 18.0, SD = 19.5, $N = 35$) ($P < 0.01$, Mann-Whitney U). Marked left-right asymmetry in palpal insertion attempts was observed in two successful copulation attempts ($E6 \times E11$, $E3 \times E11$); in both cases the left palp became tangled in silk and only the right palp (with longer insertion attempt bouts than the left) achieved successful insertions. Since it was not possible to observe every insertion attempt bout carefully enough to determine whether it was successful, we could not determine the ratio of successful to unsuccessful insertion bouts for the seven successful video-recorded copulation attempts (Table 2).

During a few of the copulation attempts, the male occasionally shifted his legs and body and moved the female, usually pushing her further upwards and backwards. During nearly all the copulation attempts, the female was motionless except for occasional quivering of her legs and pedipalps. On only three or four occasions during the 21 copulation attempts we observed did the female perceptibly shift her legs and body position. Female quivering was most likely to occur at the very beginning of a copulation period, during pauses within or between palpal insertion attempt bouts, and was more common during unsuccessful copulations than during successful ones. The longest and most intense female quivering (three long periods of especially high amplitude whole-body quivering) occurred during one short (4.47 min) unsuccessful copulation attempt ($E5 \times E11$).

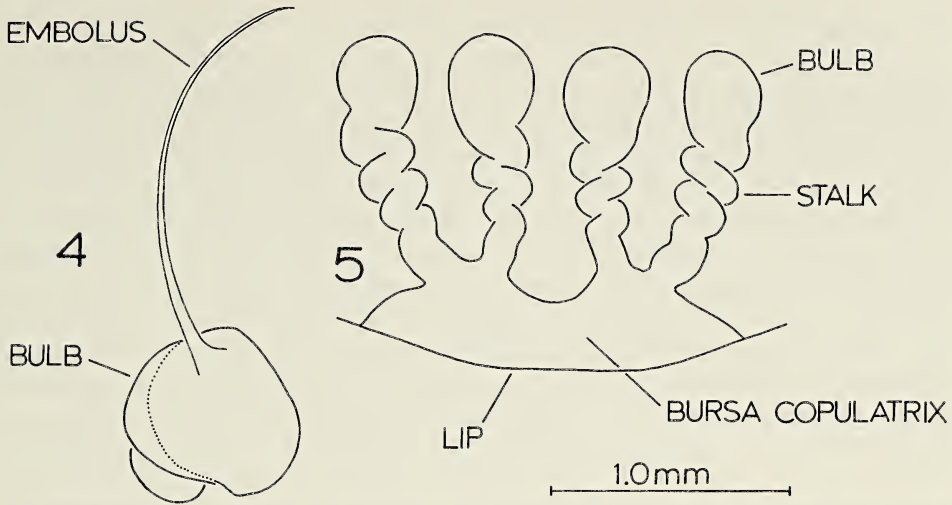
Approximately equal numbers of male uncouplings and female uncouplings followed both successful and unsuccessful copulations (Table 2). None of the uncouplings was followed immediately by a female attack. Following three of the male-initiated uncouplings, the female remained cataleptic for at least 2 s.

A survey of the structure of the palpal organ and spermathecae of *T. karshci* demonstrates that the embolus, when fully inserted into the genital opening during the successful insertion attempts described above (Fig. 2), should extend far into one of the four spermathecal stalks and possibly into the bulb (Figs. 4, 5). The curved, slender, and semi-flexible nature of the embolus may permit it to conform to the lumen of the spiraled spermathecal stalk as it is inserted and/or the stalk may be flexible enough to uncoil at least partly during this insertion. Of the eight females with sperm, five had all four spermathecal stalks and bulbs filled; the other three each had one stalk/bulb unit empty of sperm and the other three filled.

DISCUSSION

Our field data hint that male maturation in *T. karschi* may be regulated so that mating occurs just before or during the rainy season, but the Humboldt Museum (Berlin) collection contains a large number of males collected in 1907 by Scheffler just 40 miles north of population E between July and October in the dry season. The apparent high ratio of adult females to adult males observed in population E during the breeding season is probably characteristic of mygalomorph spiders in general and may, because of the increased mating opportunities for males, have important effects on their courtship and mating strategies (Coyle 1986b).

Although we did not design this study to test rigorously for behavioral isolation among the populations observed, two results provide support for the hypothesis that these populations are conspecific: 1) the absence of obvious



Figures 4-5.—Male and female genital organs of *Thelechoris karschi* drawn to same scale. 4, left male palpal organ, ventral and slightly retrolateral view with the embolus in horizontal plane. 5, female genitalia showing outline of anterior genital lip, bursa copulatrix, and the four spermathecae with coiled stalks and bulbs in horizontal plane.

differences in courtship signals among the males (populations A, C, D, and E) and females (populations B, D, E, F, G, and H), and 2) the presence of palpal insertions between individuals from populations A and E, B and E, C and E, D and E, and E and G. The low frequency (31%) of encounters resulting in copulation attempts is perhaps not surprising in view of the unknown and surely varied reproductive histories of the subjects, the 2- to 23-week hiatus between collection and observation, and the lack of strictly natural conditions.

The possible functions and origins of the courtship behavior patterns of *T. karschi* deserve comment. The male quivers and advances are probably distinct enough from prey struggles to generate vibrations that inhibit the predatory response of receptive females, and the female quiver response appears to encourage the male to continue courting. Such vibratory courtship signals are common among spiders and may, as Robinson and Robinson (1980) suggest, be ritualized conflict behaviors shaped from locomotor hesitancy in situations where both attack and flee control centers are active. Lunging appears to be ritualized agonistic behavior and, as we suggest later, may play a role in assessment of male fitness. The same may be true of leg fencing, but its function and origin might be more closely linked to clasping behavior. The female silk-walk, which appears to foster renewed male courting after a retreat from contact courtship, might be ritualized web maintenance behavior. Clasping, a male mating behavior widespread among mygalomorph taxa, may serve to protect the male, to position and steady the mating pair for more effective sperm transfer, and/or to convince the female to permit palpal insertions (Eberhard 1985; Coyle 1986). The rejection of male E6's palpal insertion attempt by female E17, when only one of his two claspers was positioned properly, supports the third function. Clasping may be a ritualized form of the defensive rearing response common to virtually all mygalomorphs. Male palpal tapping during leg fencing and clasper positioning may help convince the female to permit clasping.

A number of the courtship and mating behavior units of *T. karschi* are similar in form, context, and presumably function (and are perhaps homologous) to behaviors observed in one or more of the four other diplurid taxa whose courtship and mating behaviors have been described (*Microhexura montivaga* (Coyle 1985), *Euagrus* (Coyle 1986b), *Australothele jamiesoni* (Raven 1988), and *Phyxioschema suthopia* (Raven and Schwendinger 1989)). Males of at least the first three of these taxa rely upon similar vibratory signals, especially jerking and quivering. The "jerking bouts" of *M. montivaga*, the "jerk-quivers" of *Euagrus*, and the body jerking and anterior leg-trembling behavior of *A. jamiesoni* involve more vigorous up and down motion of the whole body and are more stereotyped than the quivering and twitching patterns of *T. karschi*. Perhaps the tapping/drumming of pedipalps by *T. karschi* males is homologous to the pedipalpal drumming performed by *A. jamiesoni*. Leg fencing appears similar to the "leg-grappling" of *M. montivaga*, and resembles the onset of clasping in *Euagrus* and *A. jamiesoni*. The drumming and quivering of pedipalps and first legs by *Euagrus* females occurs in the same context (serves the same function?) as the tapping, quivering, twitching, and jerking behavior of *T. karschi* females. Behavior resembling the silk-walking of *T. karschi* females has been observed during unsuccessful *M. montivaga* courtships but not at all in *Euagrus* or *A. jamiesoni*. The mating posture of *T. karschi* is the front-to-front posture typical of non-araneomorph spiders; in its details it is much more similar to that of *M. montivaga* than to the postures observed in *Euagrus*, *A. jamiesoni*, and *P. suthopia*, all of which employ mating claspers found on the male's second leg. The female catalepsis and alternate palpal insertion attempts characteristic of *T. karschi* copulation attempts were observed in *M. montivaga* and *Euagrus* (catalepsis) and in *M. montivaga* and *A. jamiesoni* (alternate insertions).

It is important to realize that the risk to *T. karschi* males of female-inflicted attacks and injury is probably lower in nature than in the confines of a mating arena. Although the data suggest that males are at risk during all stages of courtship and mating, from the time they enter the female's web until they depart, they also indicate that *T. karschi* males are not in as much danger of attack immediately after uncoupling as are the males of *Euagrus* and *P. suthopia* (Coyle 1986b; Raven and Schwendinger 1989).

The occurrence of both aggression-rich and aggression-poor successful courtships in *T. karschi* is of particular interest. Although the aggressive behaviors (lunging and leg-fencing) appear to be ritualized and therefore not very risky, they may increase the cost (in time and energy) of aggression-rich courtships when compared to the aggression-poor courtships. The proclivity of *T. karschi* males to lunge at females and to continue or resume courting in spite of female lunges and chases is a phenomenon not yet observed in other diplurids (Coyle 1985, 1986b, in prep.; Raven 1988). Perhaps these hawk-like interactions are fostered by females (who tend to lunge more often than the males) and serve to test the males' fitness. The sudden drastic decrease of aggression twice observed in the second consecutive courtship of a pair (E6 \times E11) might indicate that once a male has "convinced" a female that he is fit, she no longer tests him. Possibly leg fencing bouts constitute a more highly ritualized test of aggressive fitness than lunges, and supply the female with adequate fitness information in those courtship encounters devoid of lunges. Alternatively, it may be true that the observed variation in aggression is the result of variation in female receptivity

caused by habituation or other factors not necessarily related to sexual selection by female choice.

The observed willingness of female *T. karschi* to accept copulation attempts from more than one male is a prerequisite for sexual selection of male anatomical and behavioral traits associated with clasping and copulation (Eberhard 1985). Our observations that a female may reject a male which has not "properly" clasped her ($E6 \times E17$) and that palpal insertion attempts often do not lead to successful insertion are consistent with Eberhard's hypothesis that sexual selection by female choice commonly occurs during copulation attempts. It is possible that the female, even though largely cataleptic, may be providing mechanical challenges to the male's copulatory ability, monitoring his performance, and adjusting her behavior and/or physiology to maximize her fitness. If this is not happening, it seems even harder to understand why such a large fraction of palpal insertion attempts are unsuccessful and why females sometime quiver during pauses in male activity within copulation attempts.

The ability of *T. karschi* males to attempt copulations repeatedly over a period of days with different females is consistent with the apparent high ratio of adult females to adult males, with observations of other diplurids (Coyle 1985, 1986b, in prep.), and with the general pattern of male promiscuity in animals. It is not so easy, however, to understand why males which have achieved successful insertions in one copulation bout will continue to court and attempt additional copulations with the same female unless sperm is not always transferred during a successful insertion or unless, as our observations suggest, a single successful insertion (and sperm transfer) bout is not sufficient to fill all four of his mate's spermathecae. If either or both of these constraints exist, a large number of copulation attempts might be required to fill her spermathecae sufficiently to 1) fertilize all of her eggs and/or 2) inhibit her motivation to mate with other males (and, therefore, to guarantee his paternity).

We suspect that the mechanics of sperm transfer in *T. karschi* make it difficult for a male to fill all four of a female's spermathecae in one copulation attempt. Given the long embolus, the dimensions of the bursa copulatrix and spermathecae (Figs. 4, 5), the observation that the entire embolus is inserted, and the observation that the embolus is not withdrawn during an insertion bout, each successful palpal insertion bout can probably deliver sperm to only one of the four bulbs. Add to this the additional possibilities that 1) the male may have difficulty directing the embolus tip into a particular unfilled stalk at will and 2) the right pedipalp is probably designed to insert into the pair of spermathecae on one side and the left pedipalp into the other pair, and it becomes even more apparent why it might normally take more than one copulation attempt for a male to fill all four spermathecae.

In general, our observations of *T. karschi* behavior suggest that the functions of courtship may continue to be performed after the onset of clasping and during the copulation attempt that follows. The large amount of copulatory effort required per successful insertion may be partly the result of this spider's genital morphology or of female testing of male copulatory performance or both. Clearly much more information is needed about the physiology and functional morphology of reproduction and about the behavioral ecology of natural populations of this species before our observations can be understood and the questions they have generated can be answered.

ACKNOWLEDGMENTS

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THE AMINO ACID COMPOSITION OF MAJOR AMPULLATE GLAND SILK (DRAGLINE) OF *NEPHILA CLAVIPES* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT

Amino acid composition of major ampullate gland silk (dragline) produced by the mature, female golden orb-weaving spider, *Nephila clavipes* was determined. Several solvents were applied in order to solubilize the spider silk. Although several strong acids and bases were able to solubilize silk, the protein was apparently degraded by this treatment, as demonstrated by protein gel electrophoresis. Only a mixture of hydrochloric/propionic acid (50:50, v:v, final concentration 3N HCL/25% propionic acid) solubilized the silk while retaining the molecular weight integrity of the crystalline polymer. The results show that the major ampullate gland secretion is characterized by a high degree of small side chain amino acids (Ala, Gly, and Ser) and polar residues (Gly and Arg), comprising almost 75% of the total amino acids present. Contrary to published findings (Work and Young 1987), the composition of major ampullate gland silk appears to be uniform within the species. The composition of the secretion is discussed in relation to the known and implied functions of the major ampullate gland as well as in relation to the mechanical properties of the silk produced by orb-web building spiders.

INTRODUCTION

Spiders are unique in their ability to synthesize and utilize silks for a variety of purposes. The orb-web spinners are equipped with 5-7 different types of silk secreting glands, each synthesizing its own type of silk to be utilized for a specific purpose, e.g., construction of the dry and sticky parts of the web, construction of the egg-sac, and swathing silk of captured prey (Gosline et al. 1984). These fibers are synthesized by extremely specialized glands situated in the abdominal cavity. Although the amino acid composition is known for the seven silks from one animal (Andersen 1970), only two of the seven types of silk have been investigated in any detail. *Nephila clavipes* is a large, orb-weaving spider, dispersed in the tropical and subtropical areas of the western hemisphere (Moore 1977). Their most prominent glands are a pair of large major ampullate glands which secrete the protein for dragline silk. Three morphological regions distinguish the gland: the tail, ampulla, and duct. The tail is the site of approximately 90% of the major ampullate gland's protein synthetic activity; the ampulla is a storage site for soluble dragline silk; and the duct appears to be involved with secretion and ordering of silk (Bell and Peakall 1969). It can be assumed that the mechanoelastic properties of the silk fibers correlate closely

with their functional properties and that these properties are in turn determined by their chemical composition and molecular conformation. The multiformity of material makes spider silk ideal for studies on the relationship between chemical composition, structural conformation, and mechanoelastic properties of biological fibers.

The term fibroin is often used for the silk fibers secreted by some insects and arachnids (Lucas et al. 1958). Studies on the chemistry of insect and arachnid fibroins have been previously reported by Rudall (1962), Lucas et al., (1960), Andersen (1970), Hunt (1970), Hazan et al., (1975), Tillinghast and Christenson (1984), and Work and Emerson (1987). Data on *Nephila* silk amino acid composition is limited. Amino acid composition has been reported to a lesser degree for *Nephila senegalensis* (Walkenaer) (Lucas et al. 1960), *Nephila madagascariensis* (Vinson) (Lucas et al. 1960), and *N. clavipes* (Zemlin 1967; Tillinghast and Christenson 1984). The silks of these organisms appear to be composed of anti-parallel beta-pleated sheets but have different intersheet distances (Warwicker 1960). These investigations imply that the silks vary in composition and properties, but there is insufficient information to make a definitive correlation between chemical composition and structural properties. X-ray diffraction patterns (Gosline et al. 1984, 1986) have implied that the molecular conformation of major ampullate gland fibers consists of crystalline regions dispersed in a matrix of amorphous proteinaceous material. The ratios of crystalline to amorphous regions may be a crucial factor in the assessment of physical properties of the fiber.

The objectives were to (1) develop a system by which silk fibers obtained by controlled silking could be completely solubilized while retaining the molecular weight integrity of the fiber, (2) determine the amino acid composition in major ampullate gland silk (MaAS) of *N. clavipes*, and (3) search for correlations between MaAS chemical composition and physical properties of these fibers. In this paper we describe the results of amino acid composition analysis of the dragline silk of *N. clavipes* and bring out the importance of the relationships between chemical composition and physical properties.

MATERIALS AND METHODS

Species.—Samples were collected from the following araneid species, *N. clavipes* Nephilinae were kindly supplied by Angela Choate, University of Florida, Gainesville, FLA; *Argiope aurantia* (Lucas) and *Neoscona domiciliorum* (Hentz) were supplied by Mark Stowe, University of Florida, Gainesville, FLA. Specimens were kept alive in individual cages and fed a diet of German cockroaches, *Blattella germanica* (Blattellidae).

Silk collection.—Controlled silking was performed as described by Work and Emerson (1982). Controlled silking was restricted to the spiders which were large enough to be easily manipulated without damaging the spider. The silking procedure averaged 30 minutes and 5.0 milligrams (mg) of MaAS was routinely obtained. The mature females were continuously observed under 60X magnification to substantiate the glandular source of silk. All reeled samples were examined using a Zeiss light microscope (1250X total magnification) to ensure that there was no contamination by minor ampullate gland fibers.

Silk solubilization.—Silk samples (1.0-2.0 mg) were placed in 13 × 100 mm sterile glass borosilicate test tubes. The solvents listed in Table 1 were added to a final concentration of 1.0 ug/ul and solubility determined visually at room temperature.

Removal of solvent.—After solubilization the samples (reeled or glandular) were either dialyzed against 100 ml of 10 mM Tris-HCl, pH 7.0 for 24 h or dried immediately under vacuum (purged with argon) and reconstituted in the Tris buffer (final concentration 1 ug/ul).

Silk hydrolysis.—Major ampullate gland silk (reeled samples, 2.0 mg) were first dissolved in 2.0 ml of a hydrochloric/propionic acid mixture at room temperature for 20 min with slight vortexing. Solubilized samples (100 ul at 1.0 ug/ul) were vacuum dried in pyrolyzed vials and purged with argon gas. Hydrolysis was carried out by placing 200 ul of constant boiling 6N HCl in the bottom of the reacti-vial along with two sodium sulfite crystals. The vessel was again purged with argon gas, sealed under vacuum and placed at 150 °C for 1 hour. Argon was used as a purging gas because of its purity and because it contributes fewer artifact peaks in the subsequent analysis. Sodium sulfite is used as an oxygen scavenger and aids in the recovery of cysteine, serine, and threonine. The oxygen scavenging activity of the crystals in the reaction aids in avoiding non-specific hydrolysis of amino acid residues and subsequent amino acid degradation at the elevated temperatures (Ted Tanhauser personal communication).

Amino acid analysis.—Multiple analyses were carried out on a Waters HPLC Pico-Tag Amino Acid analysis system. The hydrolyzed samples were derivatized with phenylisothiocyanate (PITC) and these samples reconstituted in 400 ul of sample diluent. For each analysis a 50 ul injection volume was used. Amino acid standards were run with each sample. Ribonuclease A was run as an hydrolysis control.

Glandular dissection.—Major ampullate glands (tail, ampulla, and duct) were dissected out of living spiders through a 1.5 cm longitudinal incision along the ventral abdomen. The glands were removed carefully to avoid degradation of the luminal contents. The glands were immediately transferred to a medium containing 0.10M sodium chloride and 0.015 M sodium citrate (SSC). Protease inhibitors, phenylmethyl sulfonyl flouride (PMSF) at a final concentration of 6-10 mg/ml (Weber et al. 1972) and 20 units/ml of aprotonin (Piperno et al. 1979), were added to the dissection buffer to inhibit proteases released by the gastric system of the spider. Solubilization, hydrolysis, and amino acid analysis were performed as previously described.

RESULTS

Silk solubility.—Of the solubilizing agents studied, only hydrochloric/propionic acid (50:50, v:v) dissolved *N. clavipes* dragline silk at room temperature with only slight agitation (Table 1). Hydrochloric acid below 6N and used alone failed to completely dissolve the silk even at elevated temperatures (data not shown). Some quarternary ammonium compounds used as commercial tissue solubilizers proved to be efficient solvents, but the solvent could not be easily removed from the solution. High concentrations of base also dissolved silk samples, although they were not used because the elevated temperatures needed for solubilization may

Table 1.—Solubility of *Nephila clavipes* dragline silk in various solvent systems. 1 = Totally insoluble, 2 = Partially soluble, some particulates, 3 = Partially soluble, no particulates, viscous suspension, 4 = Totally soluble, no particulates, clear, non-viscous.

Solvent	Solubility at room temperature
Water	—1
1N HCl	—1
2N HCl	—1
3N HCl	—1
4N HCl	—2
5N HCl	—2
6N NC ₁	—/+2
1N KOH	—1
Chloroform	—1
Ethyl alcohol 95%	—1
8M Urea	—2
50% Lithium Bromide	—2
1% SDS	—1
5% Mercaptoethanol	—1
Solvent	+3
Constant boiling 6N HCl/50% Propionic acid	+4

begin random hydrolysis of the silk backbone prior to amino acid hydrolysis. Any amino acids hydrolyzed prior to the 150 °C hydrolysis reaction may then become completely degraded at the hydrolysis step and subsequently unaccounted for in the final analysis (Ted Tanhauser personal communication).

Hydrochloric/propionic acid proved to be most suitable; it solubilized the silk immediately and more importantly retained the molecular weight integrity of the silk as determined by polyacrylamide gel electrophoresis and high performance liquid chromatography (data not shown).

Amino acid analysis.—The amino acid composition of the secretion of (MaAS) from *N. clavipes* is shown in Tables 2 and 3. Glycine, alanine, glutamic acid/ glutamine, and arginine were the most abundant amino acids, together comprising 74 percent of the total amino acids present. Generally, the major ampullate gland silk has been considered for use in the production of dragline, frame threads, and radii of the web. The dragline has a high tensile strength (198 grams per denier, gpd) and it has a rupture elongation of 18% (Zemlin 1967). The composition of the material from the large ampullate gland (pulled and glandular) generally agrees with the published analyses of dragline from *N. clavipes* (Zemlin 1967; Work and Young 1987), but some differences are observed. Work and Young 1987, report extremely low levels of asparagine, threonine, arginine and valine (0.87, 0.31, 1.37, and 0.76 respectively). We report significantly higher levels of these residues (see Table 2), theorizing that these residues play important roles in the amorphous domains of the polymer. Deoxyribonucleic acid (DNA) sequencing of the MaAS gene has confirmed the presence of these residues.

Table 3 shows the amounts of various amino acid side chains in dragline silk of *N. clavipes*. Dragline silk is composed predominantly of the small side-chain amino acids glycine, alanine, and serine, which would allow them to conform to the antiparallel beta-pleated sheet model proposed by Pauling and Corey (1953) for *Bombyx mori*. The conformational model applies only to the crystalline

Table 2.—Amino acid composition of reeled dragline silk of *Nephila clavipes*. Results expressed as residues per 100 total. Three trials each spider.

Amino acid		Spider 1	Spider 2	Spider 3
Asp/Asn	(D/N)	2.5	2.4	2.6
Glu/Gln	(E/Q)	9.1	9.0	9.2
Ser	(S)	4.5	4.5	4.4
Gly	(G)	37.0	37.3	36.9
His	(H)	0.5	0.4	0.4
Arg	(R)	7.6	7.6	7.7
Thr	(T)	1.6	1.7	1.6
Ala	(A)	21.1	21.0	21.2
Pro	(P)	4.3	4.3	4.3
Tyr	(Y)	3.0	3.0	3.2
Val	(V)	1.8	1.8	1.7
Met	(M)	0.3	0.3	0.2
Cys	(C)	0.1	0.1	< 0.1
Ile	(I)	1.0	1.0	1.0
Leu	(L)	3.8	3.7	3.7
Phe	(F)	0.7	0.7	0.7
Lys	(K)	1.0	1.0	1.0

regions of *B. mori*, which makes up approximately 40% of the total silk structure, as described by x-ray diffraction analysis (Iizuka 1965). Limited x-ray diffraction data has been reported which describes the degree of crystallinity in dragline silk of certain araneid species, (Gosline et al. 1984, 1986, 1988).

We thought it worthwhile to look at the pulled draglines from other spider species, *Argiope aurantia* and *Neoscona domiciliorum*, and look for comparisons/differences in the amino acid compositions. Reeled samples of dragline silk were prepared as previously described. Table 4 shows the differences in the amino acid composition of the various draglines as compared to *Nephila clavipes* reeled dragline. Generally, *Argiope* and *Nephila* dragline silks are quite similar, although *Nephila* contains many more arginine residues (7.6% vs 2.9%). The arginine residue appears to be an important component of the amorphous domain repeating segment, as seen in DNA sequencing of the dragline silk gene (unpublished data). *Neoscona* dragline also has a similar amino acid composition

Table 3.—Amounts of various amino acid side chains in reeled dragline silk of *Nephila clavipes*. Results expressed as residues per 100 total. Small side chains: gly + ala + ser, polar residues: asp + glx, basic side chains: lys + his + arg cyclic imino side chain: pro, aromatic side chain: phe + tyr, sulfur containing: met + cys, aliphatic side chain: ala + val + ile, hydroxyl side chain: ser + thr. Three trials each spider.

Dragline silk	Spider 1	Spider 2	Spider 3
Small side chains	62.28	62.92	62.59
Polar side chains	29.81	29.61	30.22
Acidic/amide side chains	11.67	11.52	11.83
Basic side chains	9.05	9.02	9.06
Cyclic imino side chain	4.3	4.34	4.28
Aromatic side chain	3.62	3.57	3.88
Sulfur containing	0.47	0.46	0.22
Aliphatic side chain	27.61	27.57	26.62
Hydroxyl side chain	6.16	6.20	6.09

Table 4.—Amino acid composition of the silk gland secretions of various spiders. Results expressed as residues per 100 total residues.

Amino acid	<i>Nephila clavipes</i>		<i>Argiope aurantia</i>	<i>Neoscona domiciliorum</i>
	Dragline (reeled)	Glandular (MaAs)	Dragline (reeled)	Dragline (reeled)
Asx	2.5	2.1	1.6	0.6
Glx	9.2	8.3	11.1	10.0
Ser	4.5	3.9	5.1	6.8
Gly	37.1	38.1	34.7	38.0
Arg	7.6	7.2	2.9	0.6
Thr	1.7	2.0	0.8	0.9
Ala	21.1	23.4	22.2	18.0
Pro	4.3	3.9	6.4	11.2
Tyr	2.9	4.3	3.8	3.7
Val	1.8	1.7	1.5	0.7
Met	0.4	0.4	0.3	0.2
Cys	0.1	0.9	0.3	0.7
Ile	0.9	0.5	0.8	0.5
Leu	3.8	4.0	4.2	1.2
Lys	0.5	1.0	0.5	0.2

profile to *Nephila*, but does contain almost three times as many proline residues (4.3% vs 11.2%).

Table 4 also compares the amino acid composition between reeled and glandular sources of *Nephila clavipes* dragline silk. The data clearly shows the profiles are virtually identical in composition. Samples were prepared for analysis as described in materials and methods.

DISCUSSION

One of the most difficult problems in the study of structural proteins (e.g., silk, collagen, elastin, resilin, and keratin) is solubilization without degradation of the polymer (Lucas et al. 1958). *N. clavipes* dragline silk, like other insect and arachnid fibroins, does not dissolve in water; nor does it solubilize at room temperature in most of the solvents described in Table 1, except for the strong acids and Soluene. Soluene could not conveniently be removed from the silk solution and was deemed unsuitable in any further analysis.

The solubilization effect of hydrochloric/propionic acid treatment on spider silk is almost instantaneous at room temperature. Hydrolysis of the protein backbone does not appear to take place as a result of solubilization in strong acids (6N HCL/Propionic acid). The molecular weight integrity of the polymer was maintained as observed by polyacrylamide gel electrophoresis; a single, homogeneous band of approximately 350,000 daltons was observed, in both acid solubilized reeled silk and from luminal contents isolated from dissected major ampullate glands. Hydrochloric/propionic acid may act as a strong oxidizing agent. The amino acids most affected by oxidation are cysteine, methionine, and tyrosine. Cysteine was initially presumed to be destroyed over time, but the use of hydrolysis controls in the analysis indicated this was not the case. More importantly, it appears that disulfide bridges do not play a role in maintaining

the structural integrity of silk for two reasons: (1) the overall absence of cysteine (<0.50%) in the amino acid analysis, and (2) the insolubility of the silk in mercaptoethanol. Methionine also appears to have little influence on the secondary structure, since the total amount of this amino acid (< 0.50%) is too small and methionine is not implicated in crosslinking in any characterized protein.

The content of tyrosine, however, is more interesting. This amino acid residue appears unaffected in dragline silk hydrolysis and analysis (3.0%). Two plausible hypotheses may be presented, both indicating that tyrosine plays a specific role in preserving the secondary structure of spider silk: (i) spider silk tyrosine is protected against oxidation either by its position inside the hydrophobic moiety of the molecule, or by an electrophilic substitution at the e1 or e2 positions of the phenolic hydroxyl, (ii) any oxidized tyrosines are not completely degraded and complexed in the derivatization reaction, thus remaining unseparated from tyrosine in subsequent analysis. The latter seems unlikely due to the presence of oxygen scavengers in the hydrolysis reaction, which aid in recovery of certain amino acids. The former appears to be logical explanation. Parallel experiments were performed omitting sodium sulfite and hydrolysis controls; subsequently the recovery of tyrosine was unaffected by potential oxidation reactions.

The insolubility of spider silk in 8M urea, 50% lithium bromide, and 1% sodium dodecyl sulfate (Table 1) implies that hydrogen bonding may not be the only mechanism involved in intra-sheet associations between silk molecules, (Seifter and Gallup 1966). This suggests that specific bonding mechanisms which may hold the structure of the fibroin together are unaffected by this treatment. Shaw (1964) and Lucas (1966) have conjectured on the nature of silk intra-sheet bonding, but specific structural and chemical information is still lacking. The absence of cysteine and methionine in the composition of *N. clavipes* dragline silk seems to negate their possible role in the cross-linking of the silk chains. More consistent conclusions are offered by Seifter and Gallup (1966), who state that the structure of silk fibroins may consist of multiple protein regions joined by very specific chemical cross-linkages, although the association between individual silk molecules probably involves both covalent and non-covalent interactions.

The amino acid composition of *N. clavipes* dragline silk depicted in Table 2 shows a uniform trend in chemical composition. In order to determine whether these trends were actually uniform in nature, each spider was silked on three separate occasions as previously described and analyzed in triplicate to yield 9 determinations per spider species. Examination of the data from samples taken from *N. clavipes* show distinct, uniform trends in chemical composition. A wide variation in MaAS amino acid composition was previously reported by Work and Young (1987). It was our conclusion that the lack of variability in the present study was due to the use of extremely sensitive and well defined analytical techniques, high quality instrumentation and the absence of contamination by other silks (e.g., Minor ampullate gland silk). It was therefore concluded that the data illustrates substantial continuity in the chemical composition of major ampullate gland silk from *N. clavipes*.

Table 5 shows the differences in amino acid composition between *B. mori* silk fibroin (cocoon) and *N. clavipes* silk fibroin (MaAS). It can be observed that the composition of the two types of silks differ not only in relative percentages of individual residues, but also in residues present/absent. Two features of the

Table 5.—Comparative data on *Bombyx mori* and *Nephila clavipes* silk fibroins. Data on *B. mori* from Lucas et al. (1955).

Amino acid	<i>Bombyx mori</i>	<i>Nephila clavipes</i> (reeled)
Gly	44.1	37.1
Ala	29.7	21.2
Ser	12.4	4.5
Tyr, Phe	7.5	10.2
Leu, Ile, Val, Asx, Glx	3.6	11.7
Thr	1.2	1.7
Arg	1.5	7.6
Trp	0.5	N/A
Pro	ND	4.5
His, Cys, Lys	ND	1.0
TOTAL	100.0	100.0
Res, short chain (SC)	86.2	62.2
Res, long chain (LC)	13.8	29.8
Ratio (LC/SC)	0.16	0.48

analysis are worth noting; (1) the high percentage of short-chain residues in *Bombyx* fibroin (86.2%) versus *Nephila* fibroin (62.2%), and (2) the 3-fold increase in ratio of LC/SC residues in *Nephila* fibroin (0.16 vs 0.48). These findings may be critical in determining the relative ratios of crystalline-to-amorphous regions in silk, although more empirical evidence is required.

It is routinely believed that in the fibroin of the silkworm *B. mori* there is a consensus sequence of (Gly-X-Gly-X-Gly-X)_n, where X is alanine or serine, although researchers have generally differed upon the exact amino acid composition of *Bombyx* silk (Lucas et al. 1960; Iizuka 1970; Komatsu 1979; Nadiger et al. 1985). Dickerson and Geis (1969) postulated that the glycine side chains (—H) align themselves opposite alanine (—C^βH₃) or serine (—C^βH₂O₆H) side chains to conform to the anti-parallel β-pleated sheet structural model of Pauling and Corey (1953). It should be understood that this applies to the crystalline region of *Bombyx* silk as determined by x-ray diffraction patterns (Iizuka 1965). The high proportion of short side chain amino acids (62%) in the MaAS make it more conceivable for the fiber to attain the conformational structure of the anti-parallel β-pleated sheet. This predicted condition is purely theoretical because the ratios of crystalline-to-amorphous regions in both *B. mori* cocoon silk and *N. clavipes* dragline silk are currently unknown. One can assume that the relative amounts of crystalline and amorphous regions may be determined relative to their physio/chemical properties and their effect on the protein fiber. These assumptions are substantiated by the early work on fibers by Lucas et al. (1955). Interestingly enough we may equate conclusions about physical properties in which small differences induced in the chemical composition of synthetic man-made fibers (e.g., Nylon, Kevlar) translate into significant changes in the physio/chemical properties of the fiber.

The results depicted in table 4 show uniform trends, but clear differences are observed under closer scrutiny. Closer similarities are seen between *Nephila* and *Argiope* than between *Argiope* and *Neoscona* which are from the same family. Although these differences may be ecologically and/or phylogenetically-based. Further analyses of additional species is needed.

The identification of silk gene-related DNA sequences in recombinant organisms may aid in the understanding of the interaction between chemical composition/protein sequence and the exceptional physical properties conferred upon the protein fiber. Studies at the genetic, DNA/protein sequence, and transcriptional/translational control levels will further the understanding of the structure/function relationships of naturally occurring fibers.

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**COOPERATIVE FORAGING FOR
LARGE PREY BY *PARATEMNUS ELONGATUS*
(PSEUDOSCORPIONIDA, ATEMNIDAE)**

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ABSTRACT

Interrelatedness among colony members and predation competence through cooperative foraging have been proposed as factors which act to maintain an atypically high level of social organization in the pseudoscorpion, *Paratemnus elongatus*. In this paper we report on two sets of field observations consistent with these hypotheses: 1) female-bias in sex ratio, and 2) the ability of *P. elongatus* to capture unusually large, heavily-armored prey. Cooperative foraging behavior enables this pseudoscorpion to exploit ant prey (*Cephalotes atratus*) thirty times its own mass.

INTRODUCTION

Paratemnus elongatus (Banks) exhibits the highest level of social organization known among pseudoscorpions (Brach 1978). In the laboratory, immature instars communally spin and occupy silken nests used for molting, and adults and penultimate instars (tritonymphs) engage in cooperative predation (Brach 1978). These social behaviors are of particular evolutionary interest since pseudoscorpions are predominantly solitary and often intraspecifically aggressive (Weygoldt 1969; Zeh 1987). In fact, in other pseudoscorpions species, e.g., *Dinocheirus arizonensis* (Banks) and *Parachelifer hubbardi* (Banks) from Arizona, and *Cordylochernes scorpoides* (L.) and *Semeiochernes armiger* (Balzan) from Panama, we have observed numerous instances of cannibalism involving adults and nymphs preying upon same or earlier stage instars in both field and laboratory situations (personal observations).

Brach (1978) speculated that the evolution of cooperative behavior in *P. elongatus* was linked to both interrelatedness among colony members and enhanced foraging proficiency resulting from group predation. Here we provide the first quantitative data on colony composition and sex ratio in *P. elongatus* and describe field observations of cooperative foraging behavior which lend support to Brach's hypothesis.

METHODS

Between April 1988 and December 1989 we collected *P. elongatus* from beneath the bark of live or recently fallen trees, including *Miconia argentea*, *Bursera simaruba*, and *Tetrathylacium johansenii*. The pseudoscorpions generally occurred in discrete clusters (colonies) beneath sections of bark. Collections were made by brushing whole colonies into a plastic bag held firmly against the trunk of the tree. We collected them from Cerro Luisa, Gamboa, Camino de Cruces Trail, Barro Colorado Island, and Gigante Peninsula, all of which lie in tropical moist forest of the former Canal Zone, Republic of Panama. Descriptive statistics on colony composition were computed using SAS (SAS Institute, Inc. 1988). In order to test for departure from 1:1 sex ratio, we treated each colony, not individual pseudoscorpions, as a replicate. A paired *t*-test of the number of female minus male individuals in each colony was carried out on log-transformed data to equalize variance. In addition, 20 first instars (protonymphs) from three colonies were reared to adults in the laboratory to assess the correspondence between primary and adult sex ratio.

Voucher specimens of the pseudoscorpion have been deposited with W. M. Muchmore of the University of Rochester and with V. Mahnert of the Muséum d'Histoire naturelle, Switzerland. Both taxonomists have indicated that species identification of this pseudoscorpion is tentative. *Paratemnus elongatus*, which has been recorded from southeastern U.S.A., Central America, Dominica, and northern South America, is very similar morphologically to *P. nidificator* (Balzan) from Paraguay and *P. minor* (Balzan) from Brazil, and Mahnert believes that further study may show the three species to be synonymous (personal communication).

Observations and photographs of foraging behavior in *P. elongatus* were taken over a two-week period in April and May 1988. Seven colonies of pseudoscorpions had become naturally established over a 60 m section of chain-link fence immediately adjacent to second-growth forest in Gamboa, Panama. The colonies were located beneath gaps in metal sleeves connecting upright fence posts to the top horizontal bar. A common prey item of the pseudoscorpions was *Cephalotes atratus* (L.). Voucher specimens of the ant have been deposited with D. Quintero of the University of Panama.

A sample of ants and pseudoscorpions was dried at 50 °C to constant weight (Cahn 28 Automatic Electrobalance) in order to compare the relative mass of prey and predator.

RESULTS AND DISCUSSION

Colony composition.—Total number of individuals per collection varied between one and 53 with a mean (\pm SE) of 11.3 ± 2.3 ($N = 23$ collections). When categorized by life stage and adult sex, the mean numbers of individuals per collection are as follows: males = 1.43 ± 0.26 ; females = 3.22 ± 0.62 ; tritonymphs = 3.26 ± 0.90 ; deutonymphs = 2.70 ± 0.82 ; protonymphs = 0.65 ± 0.33 . The most striking pattern which emerged was the strong female-bias in colony sex ratio, with a mean proportion of males (p_m) = 0.31 ± 0.11 . This departure from a 1:1 sex ratio is highly significant statistically ($t = 2.56$, $P =$

0.009). Of the 20 individuals reared from protonymphs in the laboratory, there were 12 females, six males, and two deaths ($p_m = 0.33$). Taken together these data suggest that bias in the primary sex ratio and not sexual differences in mortality are the causes of the skewed adult sex ratio.

Population genetic models predict female-biased sex ratios in inbred populations since an excess of females acts to reduce local mate competition, i.e., competition for mates between related male offspring (see Hamilton 1967). Comparative data on a variety of species demonstrate a strong empirical link between inbreeding and sex ratio bias (Bulmer 1986). Thus our findings are consistent with (but do not prove) the hypothesis of interrelatedness among colony members. We are currently developing electrophoretic methods in order to more directly assess relatedness levels in this species.

Field observations of predation.—Corpses of medium- to large-sized insects (beetles, millipedes, and ants) were found with their appendages lodged within the entrances of the pseudoscorpion colonies. These included six specimens of the large, heavily-sclerotized cephalotine ant, *Cephalotes atratus* (see Corn 1980). On two occasions (1700 hours, 30 April 1988; 1730 hours, 2 May 1988), successful capture of and predation on live *C. atratus* were observed. With pedipalps extended, adult *P. elongatus* were assembled along the entrance of the colony to form a nearly continuous battery of chelae. As the ant walked across the colony entrance, several pseudoscorpions used their chelae to clamp onto the ant's forelegs (Fig. 1). The pseudoscorpions then pulled back into the colony, pinning the ant against the entrance. Tritonymphs converged on the ant within 60 s of capture and began inserting their chelicerae into articulations of the leg segments. Except for brief excursions, the pseudoscorpions remained at or within the nest entrance for at least 1 h after capture. After 3 h, tritonymphs were observed outside the entrance feeding on the abdomen of the ant. Comparative dry weight data illustrate the magnitude of the size discrepancy between prey and predator—the ants outweigh the pseudoscorpions by a factor of 30 (mean dry weight in mg: *P. elongatus* = 0.55 ± 0.03 , $N = 11$; *C. atratus* = 16.08 ± 0.75 , $N = 12$).

Observations of staged encounters made on three colonies suggest that cooperative effort is important in enabling *Paratemnus* to dispatch large prey. For each colony, a single live ant was deposited five times at the nest entrance (different ant used for each colony). Ants walking over the colony entrance escaped capture when only one pseudoscorpion managed to grasp a leg (5 of the 15 trials). Successful captures (4 of 15 trials) minimally involved three adult *Paratemnus* grasping the ant within 5 s of the first individual's attachment. In addition, ants which we forcefully dislodged from pseudoscorpions were still alive and mobile 10 min after capture, indicating that pseudoscorpions must restrain the ant for a relatively long period in order to kill it. In the remaining six trials, no pseudoscorpion was successful in grasping the leg of the ant.

Interesting observations of *Paratemnus* and *Cephalotes* have been recorded by M. L. Corn working in Colombia. Corn was perplexed by observations of *Paratemnus* sp. feeding on recently dead *C. atratus* since in other contexts this heavily-armored ant appeared to be impregnable to the attacks of predators. She observed *C. atratus* workers emerging relatively unscathed from columns of raiding army ants (*Labidus* sp.) (personal communication to W. B. Muchmore).

The potential significance of cooperative predation in *P. elongatus* is perhaps best illustrated by a quote from Oliveira and Sazima (1985): "Ants outnumber in



Figure 1.—Predation on a *Cephalotes atratus* worker by a colony of the pseudoscorpion *Paratemnus elongatus*.

individuals all other terrestrial animals and, although they represent a significant food resource, few predators regularly feed on them.” We suggest that the ability to dispatch large prey through cooperative predation has been an important factor in the ecological success of this very abundant (Hoff 1964) and widely-distributed pseudoscorpion.

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ALLOZYME VARIATION IN THE INTRODUCED SPIDER *HOLOCNEMUS PLUCHEI* (ARANEAE, PHOLCIDAE) IN CALIFORNIA

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ABSTRACT

Ten electrophoretic loci were scored for five California populations of the pholcid spider, *Holocnemus pluchei*. Two loci were variable, with two alleles present at each. Genetic differentiation among populations was weak (mean $F_{ST} = 0.116$; Nei's unbiased $D \leq 0.015$); this may be attributable to the recency of introduction and opportunities for gene flow afforded by the affinity of these spiders for urban habitats. A single population of the ecologically similar pholcid *Pholcus phalangioides* differed from *Holocnemus* at seven of 10 loci.

INTRODUCTION

The Mediterranean pholcid spider *Holocnemus pluchei* (Scopoli) was recently introduced into the United States. The oldest reliable North American record known to us is an observation by W. R. Icenogle in Sutter Co., California in 1974 (S. Frommer pers. comm.). It is quite possible that *Holocnemus* was introduced into the state prior to 1974 but escaped attention because it superficially resembles another pholcid, *Pholcus phalangioides* (Fuesslin). In California, *Holocnemus* occurs in high densities below 500 m elevation in cities and towns in southern California and in the Central Valley. It is particularly common around buildings, and liable to be transported passively in truck and railroad cargo. We have seen small colonies as far east as Las Cruces, New Mexico.

Jakob and Dingle (1990) found statistically significant differences in development time and body size among broods of *H. pulchei* reared under identical conditions. Spiders in the field also show a wide range of phenotypic behavioral variation, including solitary living and group living (Jakob 1989, 1991). Here we report the genetic population structure of *Holocnemus* in California; the elucidation of genetic differentiation within and among

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Figure 1.—Collecting localities for *Holocnemus pluchei* in California.

populations provides an important context in which to study evolutionary processes. Because material was readily available, we also report the genetic distance between *Holocnemus* and *Pholcus phalangioides*, a phenotypically and ecologically similar spider also introduced from Europe.

METHODS

The *Holocnemus* populations surveyed are shown in Fig. 1; these were collected from university campuses and apartment buildings at five sites in California. *Pholcus* were collected in Wisconsin and mailed to Davis. In addition, *Holocnemus* broods reared from field collected egg sacs were assayed at polymorphic loci for evidence of Mendelian ratios, as an indication that the electromorphs represented heritable variants. All spiders were starved for one week prior to analysis to ensure that prey enzymes would be fully digested.

We used the electrophoresis protocol of Ayala et al. (1972). Thirteen enzyme systems were surveyed (Table 1). The computer program BIOSYS-1 (Swofford

Table 1.—Enzyme systems surveyed, with Enzyme Commission Numbers.

Enzyme	Abbreviation	E.C. #
Adenylate kinase	AK	2.7.4.7
Aldolase	ALDO	4.1.2.13
Fumarase	FUM	4.2.1.2
Glutamic-oxaloacetic transaminase	GOT	2.6.1.1
Glyceraldehyde-3-phosphate dehydrogenase	GAPDH	1.2.1.12
α -Glycerophosphate dehydrogenase	α -GPD	1.1.1.8
Hexokinase	HK	2.7.1.1
Isocitrate dehydrogenase	IDH	1.1.1.42
Malate dehydrogenase	MDH	1.1.1.37
Malic enzyme	ME	1.1.1.40
Phosphoglucose isomerase	PGI	5.3.1.9
Phosphoglucomutase	PGM	2.7.5.1
Superoxide dismutase	SOD	1.15.1.1

and Selander 1981) was used for the genetic analyses. χ^2 procedures were used to test for deviations from Hardy-Weinberg expectations. Genetic variability scores (heterozygosity and polymorphic loci) provide an estimate of the degree of variation available for evolutionary change in populations. We report two standard heterozygosity scores: observed heterozygosity (H_{obs}) is the proportion of loci found to be heterozygous by direct observation of genotypic frequencies; expected heterozygosity (H_{exp}) is the proportion of heterozygotes calculated from allelic frequencies under the expectation of Hardy-Weinberg ratios of genotypic frequencies. We also report the percent of loci we observed to be polymorphic (P) in each population, and provide a rough comparison of these statistics to those of other spiders.

Divergence among populations was analyzed using Nei's (1978) unbiased genetic distance, which adjusts for small and variable sample sizes, and also using Wright's (1931) F_{ST} . F_{ST} is an estimate of the component of overall genetic variance attributable to among-population effects, standardized by the total genetic variance available. F_{ST} can be related directly to important homogenizing and differentiating influences of gene flow, natural selection, and genetic drift. Differentiation is strong when $F_{ST} > 0.33$: above this level, the effects of homogenizing factors (gene flow and balancing selection) become relatively unimportant in determining differences among populations (see Wright [1978] and Slatkin [1985] for discussion). The mathematical definitions of the population genetic parameters reported here can be found in any introductory population genetics textbook (e.g., Hedrick 1985).

RESULTS AND DISCUSSION

We were able to stain and reliably score 10 loci (GAPDH, GOT-1, GOT-2, HK, IDH-1, MDH-1, MDH-2, PGI, PGM, and 6-PGD; where "1" is the fastest locus migrating in the cathodal direction). In *Holocnemus*, two of these loci were variable (GOT-1, PGI) with two alleles each; the remainder were fixed for the same allele in all populations. Allelic frequencies for the variable loci are given in Table 2; genotypic frequencies did not deviate from Hardy-Weinberg expectations. The reared broods assayed for GOT-1 and PGI showed Mendelian

Table 2.—Animals sampled (N) and allelic frequencies for variable loci in *Holocnemus pluchei* populations. Allele F migrates fast cathodally, S is slower.

Population	N	Locus and allele			
		GOT-1		PGI	
		F	S	F	S
Davis	29	0.603	0.397	0.879	0.121
Fresno	20	0.684	0.316	0.975	0.025
Bakersfield	19	0.947	0.053	0.765	0.235
Newhall	15	1.000	0.000	0.893	0.107
Riverside	19	0.816	0.184	0.971	0.029

ratios in most cases where variability was present (Table 3). However, Brood 1 deviated from Mendelian ratios at GOT-1; this may have been due to multiple mating with males of different GOT-1 genotypes, but if so, the genotypic ratio at PGI indicates that all the fathers were PGI heterozygotes. No field data concerning the frequency of multiple mating are available.

Genetic variability scores for all populations are shown in Table 4. Genetic distances between *Holocnemus* populations are quite low (Table 5), and analysis using F_{ST} indicates that the relative genetic differentiation among populations is biologically minor (GOT-1: $F_{ST} = 0.148$; PGI: $F_{ST} = 0.063$; mean $F_{ST} = 0.116$). As a comparison, mean $F_{ST} = 0.009$ among sample populations of the eastern North American monarch butterfly (Eanes and Koehn 1978), which is essentially panmictic; $F_{ST} = 0.705$ among sample populations of a plethodontid salamander (Wake and Yanev 1986). The genetic distance between *Pholcus* and *Holocnemus* is high (Table 5); these taxa show fixed differences at seven of the ten loci scored (GAPDH, GOT-2, HK, IDH-1, MDH-1, PGI, 6-PGD), suggesting a very old divergence between these ecologically rather similar species.

While genetic variability in *Holocnemus pluchei* is low relative to most invertebrate species examined (Nevo 1978), it remains within the range reported in other spiders. Different heterozygosity parameters used in the arachnological literature makes comparison difficult, permitting only a rough sense of the reported range of variability: heterozygosities (H_{obs} and H_{exp}) from the literature range from a low of 0.017 in *Anelosimus eximius* (H_{exp} ; Smith 1986) to a high of 0.094 in *Araneus ventricosus* (H_{obs} ; Manchenko 1981). The degree of

Table 3.—Genotypic frequencies for variable loci in broods reared from wild-collected females. Only brood 6 at GOT-1 differs significantly from Mendelian expectations ($P < 0.0001$; see text).

Genotype	1989 brood number				
	6	7	8	9	10
GOT-1					
FF	23	8	-	6	10
FS	15	-	10	4	-
SS	-	-	-	-	-
PGI					
FF	11	8	10	10	5
FS	17	-	-	-	5
SS	10	-	-	-	-

Table 4.—Genetic variability scores for all populations. A = mean number of alleles per locus; H_{obs} = observed proportion of heterozygotes; H_{exp} = proportion of heterozygotes calculated from Hardy-Weinberg proportions; P = percent of loci polymorphic, with more than one allele detected. Standard errors in parentheses.

Population	A	H_{obs}	H_{exp}	P
Davis	1.2 (0.1)	0.083 (0.061)	0.070 (0.051)	20.0
Fresno	1.2 (0.1)	0.068 (0.063)	0.049 (0.044)	20.0
Bakersfield	1.2 (0.1)	0.046 (0.036)	0.047 (0.037)	20.0
Newhall	1.1 (0.1)	0.021 (0.021)	0.020 (0.020)	10.0
Riverside	1.2 (0.1)	0.043 (0.037)	0.037 (0.031)	20.0
Wisconsin (<i>Pholcus</i>)	1.0 (0.0)	0.000 (0.000)	0.000 (0.000)	0

polymorphism (assessed as the percent of loci with more than one electromorph observed) ranges from a low of 3.9% in one population of *A. eximius* (Smith 1986) to a high of 33% in an *A. ventricosus* population (Manchenko 1981). We omit the high variability scores calculated from Pennington's (1979) genotypic frequency data because he assayed only polymorphic loci. Note however that it is not possible to generalize about variability across all spiders because most previous work concerns spiders with unusual social structures that may well influence patterns of genetic variability (see also Cesaroni et al. 1981). The high genetic similarity among *Holocnemus* populations may have up to three contributing factors. If natural selection on these loci is negligible, genetic drift alone countered by a gene exchange rate of approximately 2 individuals per generation will explain the observed level of population differentiation (using Wright's [1931] formulation $Nm \approx (1/F_{ST} - 1)/4$, where Nm is the rate of gene exchange among populations in an island model of genetic population structure; see also Slatkin and Barton [1989]). This level of gene flow is well within the range expected from the spiders' affinity for urban and suburban habitats. However, selection for balanced polymorphisms at variable loci can also promote similarity. The recency of the *Holocnemus* introduction in California may promote similarity as well: genetic drift is a function of population size, and the large population sizes in California may not have had time to fully differentiate. These latter factors, depending on their importance, will correspondingly reduce the estimate of gene flow required to explain present levels of differentiation. Repetition of this study after 10-15 years, and a study of European populations, would help to determine the relative importance of these factors.

Holocnemus is also unusual in having been recently introduced in California, and its low variability scores are perhaps to be expected: low heterozygosity in founder populations is well known (e.g., Harrison et al. 1983). Indeed, the

Table 5.—Pairwise genetic distances between populations using Nei's (1978) unbiased genetic distance.

Population	Davis	F	B	N	R
Fresno (F)	0.000				
Bakersfield (B)	0.013	0.011			
Newhall (N)	0.015	0.010	0.001		
Riverside (R)	0.004	0.001	0.005	0.003	
<i>Pholcus</i>	1.309	1.290	1.197	1.194	1.249

maximum of two alleles per locus found in this survey suggests that the original California propagule may have been as small as a single gravid female. The complete lack of genetic variability in the single *Pholcus* population may not be representative of the species as a whole, because this sample was collected from a small, isolated population.

Given the relatively low genetic variability scores and the recency of introduction into California, the differences in life history traits among families reared under identical conditions (Jakob 1989; Jakob and Dingle 1990) are striking. Such variation may result from genetic differences among families, but may also arise in part from differences in the maternal environment during egg maturation—egg size, for example, may vary depending on the mother's foraging success. Maternal effects can be quantified through more elaborate experimental designs. The wide range of behavior expressed during *H. pluchei* social interactions in the field (Jakob 1989, 1991) may be maintained in the population by genetic polymorphisms in loci which regulate such behaviors deterministically, or a "general purpose" genotype shared by all members of the population which permits the spiders to behave flexibly. To the extent that the low level of genetic variability shown in this study is representative of the genome, the second alternative seems most likely.

The low variability in the loci studied does not bode well for the use of electrophoretic data for *in situ* paternity analysis or other fine-grained field studies in *Holocnemus* (c.f., Jakob 1989). However, this technique could be used under laboratory conditions to determine, for example, whether spiderlings joining groups prefer closely related individuals.

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**PARASITISM OF *NEPHILA CLAVIPES*
(ARANEAE, TETRAGNATHIDAE) BY AN ICHNEUMONID
(HYMENOPTERA, POLYSPHINCTINI) IN PANAMA**

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ABSTRACT

An apparent outbreak of *Hymenoepimecis* sp., a heretofore unknown ectoparasite of the giant orb weaver, *Nephila clavipes* is documented in Panama during 1984-1985. Parasitism was highest (25-30%) among intermediate-sized, juvenile female spiders. During the second year the wasps became less discriminating in selecting host spiders. Female wasps were significantly larger than males, and the size of the wasp ectoparasite was positively correlated with the size of the host spider. Although intermediate-sized females that had males in their webs were less likely to be parasitized than such females without males, results from an insectary experiment showed that male spiders did not prevent an established wasp larva from killing its host.

INTRODUCTION

The Pimplinae is a diverse subfamily of Ichneumonid wasps, within which the tribe Polysphinctini are ectoparasites of spiders. Currently there are no published accounts of the biology of any neotropical Polysphinctine (Wahl pers. comm.; Fitton et al. 1988), nor of their effect on the host population. In Panama we witnessed high levels of parasitism by an undescribed polysphinctine wasp, *Hymenoepimecis* sp., whose host was the golden orb weaver spider, *Nephila clavipes* (L.). Herein we describe the life cycle of the parasitoid wasp, and document the frequency of the parasitoid in the host population over a two-year period.

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MATERIALS AND METHODS

The study was conducted on Barro Colorado Island (hereafter designated BCI) in the Republic of Panama. There, the lowland moist forest experiences a dry season from January to May (see Leigh et al. 1982 for habitat description). The host spider, *Nephila clavipes*, normally has two generations per year, with mature adults peaking in early wet season and in late wet to early dry season (Lubin 1978; Vollrath 1980).

The frequency of *Hymenoepimecis* sp. on *N. clavipes* was measured during two study periods that encompassed both dry and wet seasons in 2 consecutive years; from March to August 1984, and from February to December 1985. In 1984 *N. clavipes* was sampled by noting individuals encountered along roughly 1.5 km of trails transecting mature forests, and in the clearings adjacent to these trails. We marked the location of the web and measured the total length of the spider's cephalothorax-abdomen with calipers, recorded the number of males present in the web, and noted the presence of any parasitoid eggs or larvae on the female spider. Webs were checked on average of once every 3 days, until the spider could no longer be found in its original spot, or until the end of the study period.

In 1985, spiders were checked weekly or bi-weekly along 2 km of trails on BCI and the size of the spider was measured by the tibia-patella length. The cephalothorax-abdomen length of female spiders was highly correlated with tibia-patella length ($r = 0.96$, $N = 21$ females, $P < 0.05$). For comparisons between years, we converted body length data to estimates of tibia-patella length using the regression equation. To determine whether the outbreak was a localized phenomenon, monthly surveys of *N. clavipes* over roughly the same length of trail were conducted on the mainland peninsula of Gigante from February 1985 to February 1986.

The life cycle of the *Hymenoepimecis* sp. parasitoid was studied by maintaining field collected, parasitized spiders in an outdoor insectary ($2 \times 2 \times 2.5$ m). The spiders readily built webs and fed on small insects thrown into their webs. We measured the length of the parasitoids daily, noting when the host spider died, and when the larva pupated. The wasp pupae were removed from the webs and kept individually in small screen vials. The size and sex of the emerging adult wasps was recorded. Oviposition behavior and the reaction of female *N. clavipes* to wasps was noted opportunistically in the field.

Juvenile females with male spiders in the web were parasitized less frequently than were those in the presence of male spiders. To determine if this effect was a consequence of the male's behavior, one or two males were placed in the webs of 12 recently parasitized female spiders that were maintained in the insectary. Interactions between the parasitoids and the male spiders were noted during hour-long daily observation periods until the host spider was killed or the parasitoid disappeared.

RESULTS

Frequency and distribution of the parasitoid.—Parasitism by *Hymenoepimecis* sp. on *N. clavipes* in 1984 and 1985 is shown in Table 1. In both years, female spiders of intermediate size (corresponding to instars 5-8) were disproportionately

Table 1.—Occurrence of parasitism by *Hymenoepimecis* sp. and of males in the webs of female *N. clavipes* of different sizes. For comparison of percentage of parasitism, 1984 samples were combined.

* = The smallest instars were not sampled in 1984.

Tibia-patella length (mm)	Year	N	Parasitized		Females with males
			n	%	
≤0.4	1984 (BCI) *	18	0	0	0
	1985 (BCI)	117	7	5.9	0
	1985 (mainland)	14	0	0	0
>0.4 ≤0.7	1984 (BCI)	24	2	8.3	2
	1985 (BCI)	81	8	9.9	1
	1985 (mainland)	36	5	14.0	3
>0.7 ≤1.2	1984 (BCI)	113	29	25.0	54
	1985 (BCI)	77	23	30.0	9
	1985 (mainland)	55	8	14.6	19
>1.2	1984 (BCI)	112	1	1.0	92
	1985 (BCI)	85	1	1.2	41
	1985 (mainland)	78	0	0	50

parasitized. Most (68%) sexually mature adult *N. clavipes* females were found in association with one or more males whereas only 32% of the intermediate-sized females had males in their webs. However, only 4 of the 154 (3%) *N. clavipes* females that had males in the web were parasitized ($\chi^2 = 8.4$, $df = 1$, $P < 0.05$). Of the 5-8th instar females (i.e., those most heavily parasitized), 69 of 341 (20%) had males in the webs. Only three of these females (4%) were parasitized as opposed to a 27% parasitism rate in the 272 females (27%) that lacked males ($\chi^2 = 12.8$ $df = 1$, $P < 0.05$).

In 1985, the incidence of parasitism in the BCI sample was about twice that found in the mainland sample of *N. clavipes* (Table 1). In this year on BCI, the normal peak in abundance of mature females in December never materialized (Higgins, unpubl.). Concomitantly, ovipositing wasps were less discriminating in their selection of host spiders. Eleven juveniles too small to sex (<4 mm tibia-patella length) and 3 of the 61 juvenile males censused were parasitized. Four cases of double parasitism were also observed.

Lifecycle of *Hymenoepimecis* sp.—We do not know how *Hymenoepimecis* sp. detects *N. clavipes* hosts. However, once the wasp located a potential host, it was not always successful in parasitizing the spider. On three occasions female *N. clavipes* were found off of the web (either in the leaf litter or on a lateral branch) while the wasp rested at the web center. The spiders approached the web, plucked it, and then dropped into the leaf litter. The wasps reacted by flying off of the web, circling it, and then flying away. Two of these spiders were later found parasitized. The third already had an early instar larva attached to it. We did not witness interactions that led to a wasp successfully landing on a spider host.

Hymenoepimecis sp. appeared to temporarily paralyze its host. On one occasion a female wasp was seen to sting a spider between the sternum and the coxae (see also Nielson, 1935; Eason et al., 1967). Typically, a wasp sat on the dorsal or dorsal-lateral side of the spider's abdomen, grasping the posterior end of the abdomen with her first pair of legs (Fig. 1). The wasp then moved her ovipositor back and forth for up to 5 min before attaching a single egg the cuticle

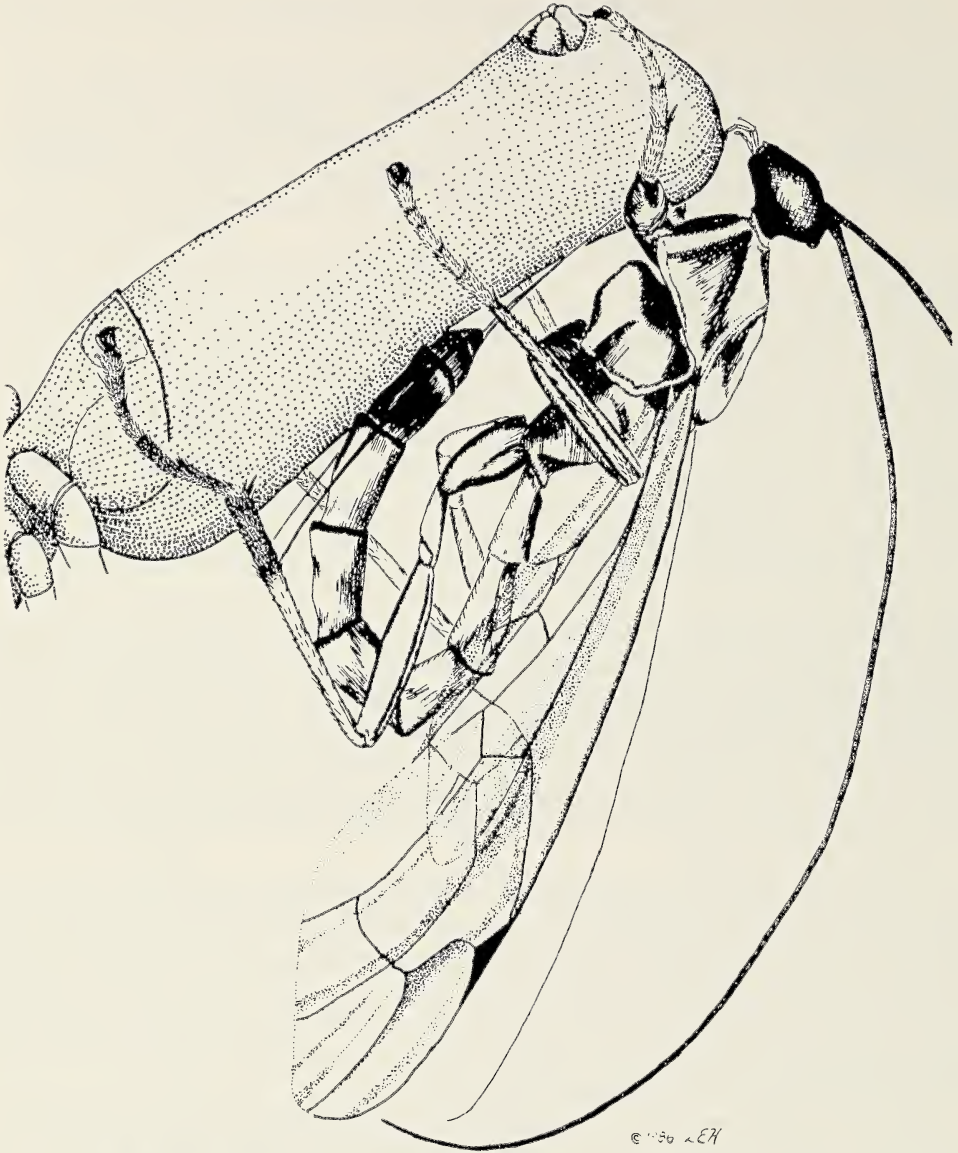


Figure 1.—A female *Hymenoepimecis* sp. ovipositing on a female *N. clavipes*.

of the spider. Fifteen min after the wasp oviposited, the host spider had fully recovered.

Within 24 h the eggs ($N = 4$) hatched into larvae roughly 1 mm in length. One newly hatched larva was unable to attach itself to the spider and died within 24 h. Although this female spider grew to maturity (at below average size), she retained a scar on the abdomen where the egg had been attached. Wasp larvae grew slowly for the first week, after which they increased rapidly in size (Figs. 2, 3). Parasitized female *N. clavipes* built increasingly irregular, reduced webs but continued to feed up to 1-2 days before they died. By the end of 2 weeks the larvae had completely sucked out their host, leaving only the exoskeleton which dropped to the ground. Three of the 25 larvae maintained in the insectary



Figure 2.—*Hymenoepimecis* sp. larva at 7 days post-hatch, attached to a female *N. clavipes*.

disappeared after killing the host. Remaining larvae took 3-5 h to build golden, spindle-shaped cocoons that hung conspicuously within the frame lines of the host web (Fig. 4).

Hymenoepimecis sp. larvae failed to complete development if the host spider was too small or if it had already been parasitized. All of the larvae on juvenile males and on the small females (<4 mm tibia-patella length) that were brought into the insectary failed to pupate before the spider died. In all four cases of double parasitism, the larger, first-laid larvae was the only one of each pair to survive (one of these larvae ate the other). Two of the 22 pupae formed in the insectary failed to emerge for unknown reasons. In the field, one pupa was eaten by a kleptoparasitic spider (*Argyrodes*), and three were found crushed by heavy rains.

Even though male *Hymenoepimecis* sp. were smaller (\bar{X} body length \pm SE = 14.8 ± 0.1 mm, $N = 6$) than the females ($\bar{X} \pm$ SE = 17.6 ± 0.1 mm, $N = 11$), the time required to emerge after pupation did not differ significantly between the sexes ($\bar{X} = 10.4 \pm 0.7$ days, $N = 5$ males; $\bar{X} = 11.0 \pm 0.4$, $N = 11$ females). The

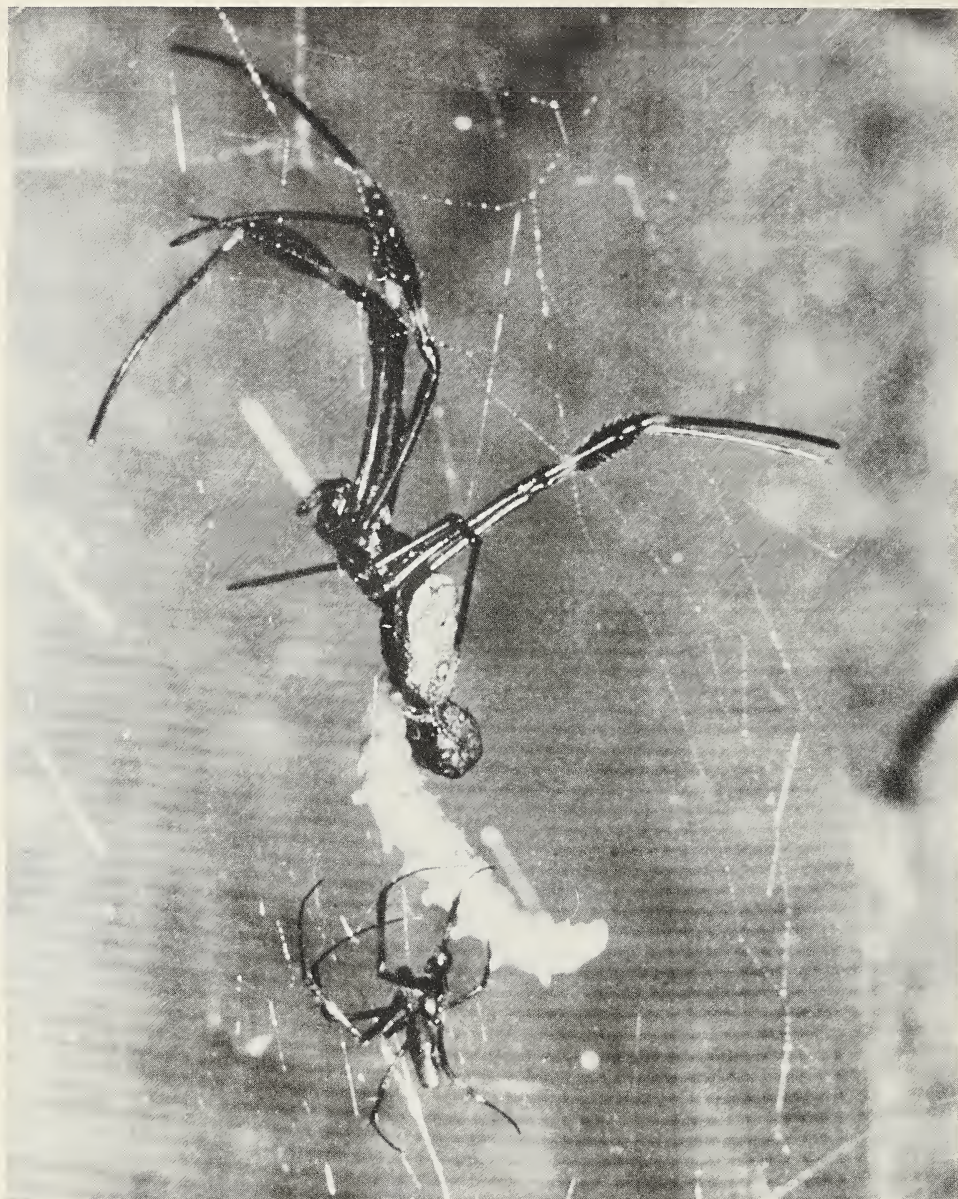


Figure 3.—Male *N. clavipes* touching a wasp larva as the larva feeds on a female *N. clavipes*. Pupation occurred 2 days later.

total time from egg to adult was 27 and 28 days for the two female wasps for which the date of oviposition was known (we lack similar data for males). Newly emerged adult *Hymenoepimecis* sp. released in the insectary with large *N. clavipes* females did not mate nor orient to any of the spiders.

In both years the sex ratio of emerging wasps was significantly biased towards females (1984, 7 males: 13 females; 1985, 6 males: 12 females, $P < 0.05$, χ^2 tests). There was a significant correlation between size of the host spider (tibia-patella length) and body length of the emerging wasp ($r = 0.91$, $N = 7$, $P < 0.05$).

Effects of male *N. clavipes* on success of the parasitoid.—In the insectary experiment, all of the 12 parasitized female spiders with male *N. clavipes* in their

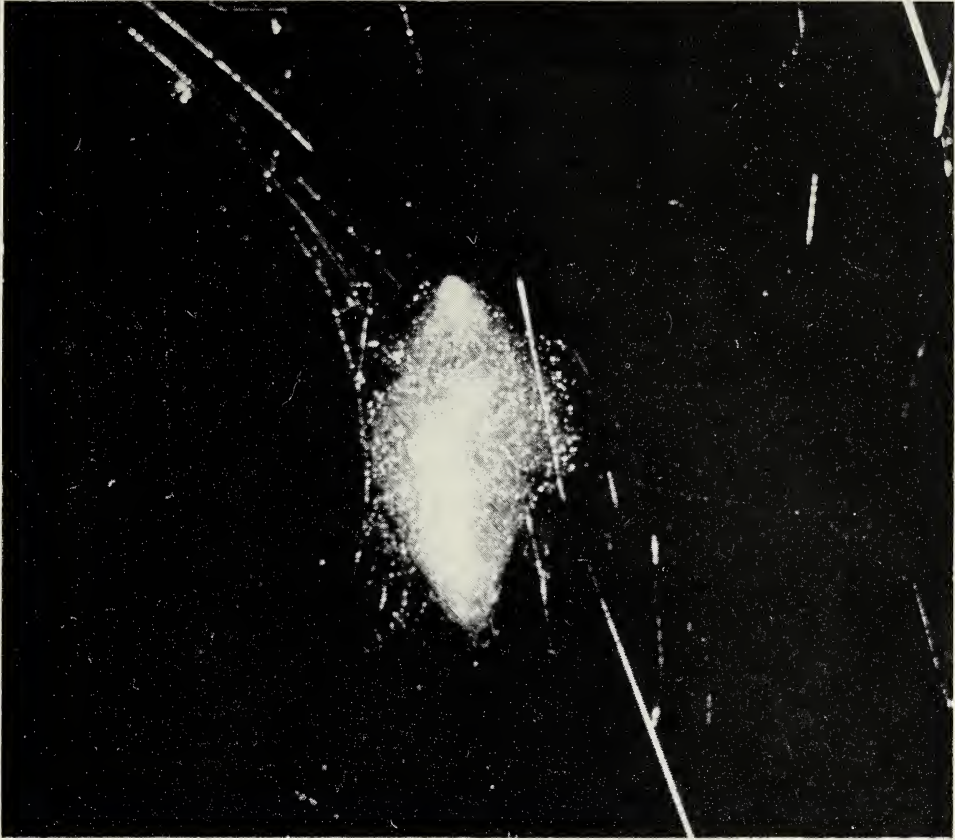


Figure 4.—Pupa of *Hymenoepimecis* sp. in the web of the dead host female *N. clavipes*.

webs were eventually killed by the parasitoids, of which all but one pupated successfully. The one exception was a larva that, after killing its host, failed to pupate before it was eaten by a second *N. clavipes* female that wandered onto the web. Periodically a larva raised its anterior end to reposition its mouth on another area of the spider's abdomen. During such times, male *N. clavipes* occasionally touched the larva (Fig. 3), but they never removed nor ate larvae. We cannot rule out the possibility that males interfere with successful oviposition by the adult wasps.

DISCUSSION

The fact that *N. clavipes* host spiders continued to build webs and feed for nearly two weeks after being parasitized indicates that *Hymenoepimecis* sp. conforms with other known polysphinctines in being koinobiotic (i.e., paralyzing their hosts only temporarily) (Askew and Shaw 1986). Many temperate polysphinctines overwinter as small instars on the spider host and develop over several months during which the host spider molts. *Hymenoepimecis* sp., however, developed rapidly and killed the host before the spider molted. The larva of some parasitoids may actively inhibit molting, but the only parasitized *N. clavipes* that we observed molting did so after losing its parasitoid. Because newly emerged female *Hymenoepimecis* sp. did not react to male wasps nor to potential

host spiders, their ovaries are probably undeveloped. The two periods during which we sampled *N. clavipes* in 1984 corresponded closely to the peaks of subadults and early adults of the biannual generations (Lubin 1978; Vollrath 1983). Unless it uses more than one host (unlikely for a koinobiotic polysphinctine, see Fitton et al. 1988), the wasp parasitoid must live at least 1-2 months in order to persist during periods of low juvenile female densities, between January and March, and August and October.

Because *Hymenoepimecis* larva were rarely seen to disappear from the host spider, we conclude that the observed size-specific parasitism did not result from differential larval success after oviposition. At present we do not know if the disproportional use of intermediate-sized spiders results from a choice preference by ovipositing wasps (e.g., Eason et al. 1967; Fitton et al. 1988) or from the superior ability of larger *N. clavipes* females to avoid ovipositing wasps. Although mature females that had male spiders in their webs suffered disproportionately less parasitism than did mature females without males, male *N. clavipes* did not interfere with successful development of the parasitoid. Limitation of parasitism of *N. clavipes* to intermediate size classes of the host spider provides one adaptive advantage to small size in male *N. clavipes*. By being too small to nourish a larva to pupation, males effectively escaped attack by the wasp. In this study, mature males were never observed to be parasitized, and juvenile males were parasitized only in late 1985, when large juvenile females were scarce.

Male *Hymenoepimecis* sp. were significantly smaller than females, and wasp size was correlated with the size of the host spider (see also Jowyk and Smilowitz 1978; Samson 1984), suggesting that an ovipositing female can assess the relative size of a potential host, and control the sex of her eggs (e.g., Cole 1981; Sandlan 1979b; Askew and Shaw 1986). *Hymenoepimecis* sp. females may assess host size and/or the presence of ectoparasitic larva by moving the ovipositor over the host's body prior to egg-laying.

Although *Hymenoepimecis* sp. becomes a large and conspicuous ectoparasite on *N. clavipes*, parasitism by these wasps has not previously been reported by other researchers working with *N. clavipes* on BCI (Robinson and Robinson 1977; Vollrath pers. comm). Nor were the ectoparasitoids noticed during three months in 1982, when *N. clavipes* webs were monitored as part of a study of spider predation by damselflies on BCI (Fincke unpub.). On mainland Panama where the density of *N. clavipes* was greater than on BCI, Vollrath (pers. comm.) found parasitoids only rarely. The high level of parasitism we found during 1984-1985 suggests that this was an uncommon outbreak of *Hymenoepimecis*. The environmental and biological factors that normally control the density of *Hymenoepimecis* sp. are unclear. In 1985 both the dry and the wet seasons were dryer than average (D. Windsor 1990). Because pupae were sometimes found to be killed by the heavy rains, the parasitoids may benefit from dry weather. Parasitism in 1984 probably contributed to the decline of the BCI *N. clavipes* population found in 1985 which was coupled with double parasitism and the use of host spiders of sub-standard size.

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ONTOGENETIC CHANGES IN THE SPINNING FIELDS OF *NUCTENEA CORNUTA* AND *NEOSCONA THEISI* (ARANEAE, ARANEIDAE)

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ABSTRACT

The postembryonic development of spinning organs of *Nuctenea cornuta* (Clerck) and *Neoscona theisi* (Walckenaer) (Araneae, Araneidae), was studied with SEM, emphasizing first appearance of, and increase in, spigot and fusule complements. Our results suggest that these species may renew their spinning fields by two distinct methods during their ontogeny: spigots may be merely molted *in situ* like any other cuticular appendage; and/or spigots in one position are lost and “replaced” by an apparently new spigot in a new position. Some or all of each class of fusule (aciniform and pyriform) as well as major and minor ampullate spigots are replaced as well as merely molted. Flagelliform and aggregate spigots seem to be merely molted, never replaced. Evidence for these modes of replacement are the apparently vestigial spinning structures that persist from the previous instar, termed “nubbins” in the case of spigots, and “tartipores” in the case of fusules, as well as patterns in the increase in numbers of fusules and spigots. Spinneret ontogeny confirms Theridiidae and Tetragnathidae as phylogenetically derived taxa relative to Araneidae.

INTRODUCTION

Previous work on spinnerets has concerned histology (see Kovoer 1987 for a review), morphology (Glatz 1967, 1972, 1973; Mikulska 1966, 1967, 1969; Wasowska 1966, 1967, 1970, 1973; Coddington 1989), and function (Peters 1983, 1984; Peters and Kovoer 1980). Relatively few studies, and none using scanning electron microscopy, have described the ontogeny of spinning organs. Mikulska (1966) compared the differences of spinning structures between the adults and subadults of *Nephila clavipes* (L.) but did not know to which instar the subadults belonged. Richter (1970a) presented a very similar work on *Pardosa amentata* (Clerck). Glatz (1972, 1973) compared the spinning structures of first instar to those of adults for several primitive spider groups. Opell (1982) described the ontogeny of only the cribellum of *Hyptiotes cavatus* (Hentz). Works on the entire postembryonic ontogeny were done by Kokocinski (1968) and Wasowska (1977).

Kokocinski used light microscopy to study the changes in the number of external spinning structures in *Agelena labyrinthica* (Clerck). Wasowska used light microscopy to describe the postembryonic morphology of the spinning apparatus in eight species belonging to seven families (Thomisidae, Lycosidae, Agelenidae, Argyronetidae, Theridiidae, Araneidae, Tetragnathidae).

In this study we observed the morphology of each instar with SEM to record detailed characters apparently missed by Kokocinski and Wasowska, who were limited to light microscopy.

For ease of discussion we maintain in this paper the distinction between fusules—multiple spigots serving either aciniform or pyriform glands, and spigots—morphologically singular spigots *per se*. Araneid spiders have five types of spigots (major ampullate, minor ampullate, cylindrical, flagelliform, aggregate) and two types of fusules (piriform, aciniform). All adults have one pair each of major ampullates, minor ampullates and flagelliforms; two pairs of aggregates, and three pairs of cylindricals. The positions of spinning structures and the topographies of adult spinnerets are diagrammed in Coddington (1989).

MATERIALS AND METHODS

Nuctenea cornuta (Clerck) and *Neoscona theisi* (Walckenaer) were studied. Both species are widely distributed in China. The specimens were collected in Wuhan City, China and reared from eggsacs by Jingzhao Zhao, Professor in the Department of Biology, Hubei University. Specimens of each instar were preserved in 75% ethanol. All specimens of one species are from the same egg sac. The number of specimens we used for each instar are given in Table 1. Vouchers are deposited in the National Museum of Natural History (USNM), Smithsonian Institution.

The methods used to prepare specimens generally follow Coddington (1989). The forceps squeeze was only used for third instar or older, as younger instars are too fragile. Younger instars are cleaned and whole abdomens mounted; careful adjustments are needed in the 100% ethanol fixing and mounting steps to ensure visibility of PMS and PLS spinnerets. Ultrasonic cleaning times differed among instars: adults ca. 60 s; fourth or fifth, ca. 30 s; third, ca. 20 s; second, 0-5 s. First instars were mounted without ultrasonic cleaning because their small bodies are easily broken.

Numbers of spigots and fusules in Table 1 are reported for one spinneret of each pair; to calculate total spinning complements, double that number. Occasionally we use this calculated total when discussing our results. When a difference in the number between the two spinnerets was found, both spinnerets of the pair were counted.

Our nomenclature for instars of spiders follows André and Jocqué (1986). We call the stage emerging from the egg the “first” instar, the one emerging from the eggsac the “second” instar, and number succeeding instars consecutively. Individuals of each species matured in either the sixth or the seventh instar. The loss of either spigots or fusules can result in vestigial structures of scars in subsequent instars. To distinguish them we call nubbins resulting from fusules “tartipores” (based on comments in Kovoov (1986) who first noticed the structures), and nubbins resulting from spigots we simply call nubbins. The figures portray either right or left spinnerets, depending on the specimen used.

Abbreviations are: AC, aciniform; AG, aggregate; ALS, anterior lateral spinnerets; CY, cylindrical; FL, flagelliform; MAP, major ampullate; mAP, minor ampullate; Nc, *Nuctenea cornuta*; Nt, *Neoscona theisi*; PI, piriform; PMS, posterior median spinnerets; PLS, posterior lateral spinnerets; tart., tartipores. Throughout the text, these abbreviations are intended to apply to spigots and their distributions only; we have no evidence regarding the ontogeny of the silk glands themselves. To make the figures more easily understandable, each also has a label of the form "Nc ♀ ALS-4." This means, e.g., *Nuctenea cornuta*, female, anterior lateral spinneret, fourth instar. The sex of the earliest instars could not be determined.

RESULTS

***Nuctenea cornuta*.**—First instars have no functional spigots or fusules (Fig. 30). Functional spinning structures first appear in second instars. Although second instars have few fusules (Figs. 1, 7, 13), they have examples of all spigots except CY (Table 1).

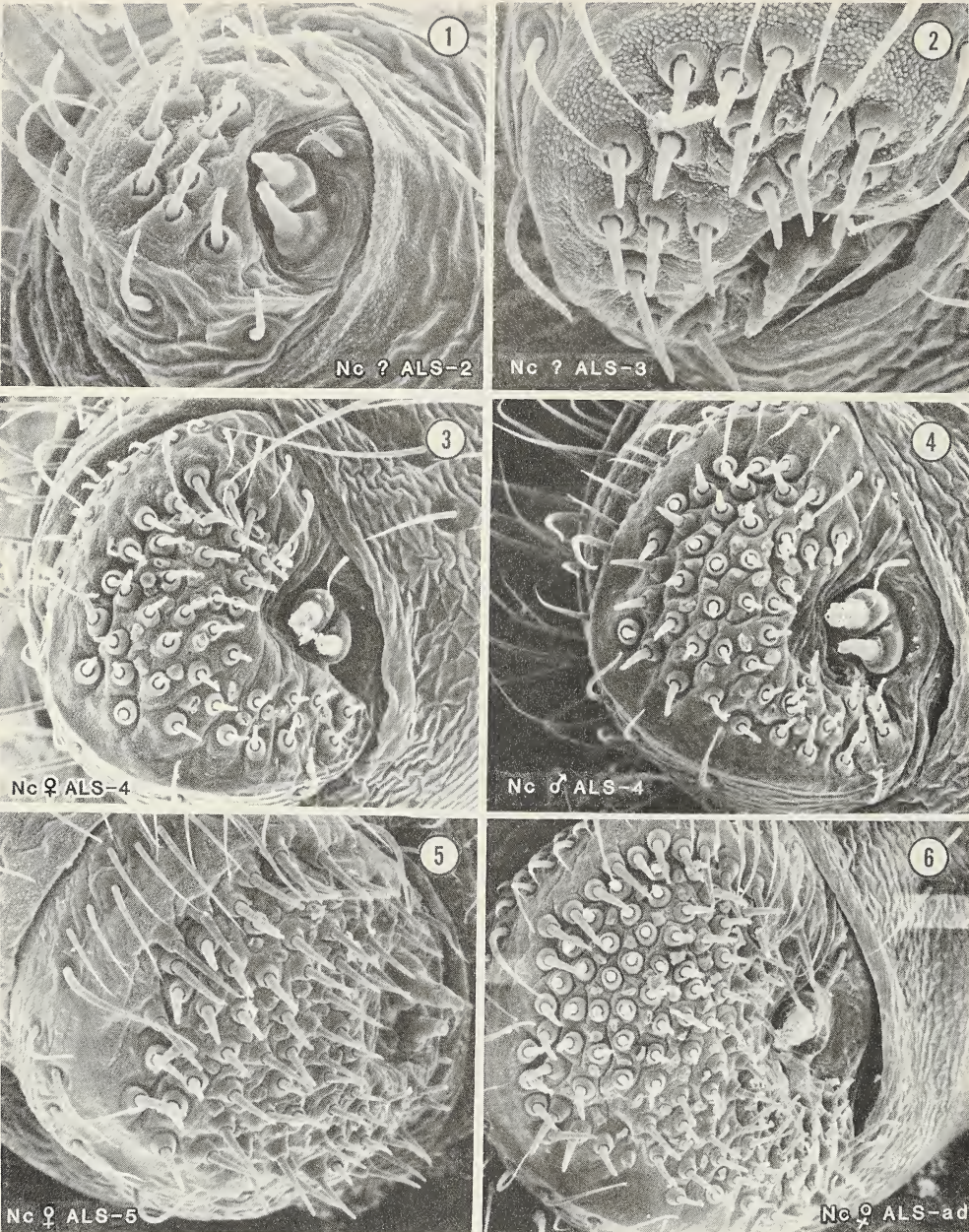
From second to fifth instars, two MAP occur on the mesal ALS margin, one anterior and one posterior (Figs. 1, 5). In second and third instars those two MAP are similar in size (Figs. 1, 2). In fourth and fifth instars the hind spigot becomes smaller and finally atrophies to become the ALS MAP spigot "nubbin" in the adult instar (Figs. 4-6).

The PMS mAP develop in a more complex pattern. Second instars have two mAP spigots per PMS (Fig. 7). The posterior spigot apparently disappears in the third and leaves a vestigial "nubbin" in its place (Fig. 8). The posterior position of the nubbin is evidence that it is indeed the posterior mAP spigot that is lost. Third instars also apparently replace the mAP spigot represented by the nubbin with a new mAP spigot between the anterior one and the posterior nubbin. In effect the posterior mAP spigot has "changed places" and left a scar in the old position. The new mAP spigot is generally smaller than the old one. The size differences are clear in fourth and fifth instars (Figs. 9-11). This new mAP spigot, which first appeared in the third instar, also disappears by the adult instar and leaves its own vestigial nubbin on the posterior PMS margin (Fig. 12). In all, 3 mAP appear on the PMS during development but two are lost. Only the most anterior, which first appeared in the second instar, persists as a functional spigot in the adult instar.

One could also interpret the nubbin that appears in the fifth and sixth instars (Figs. 11, 12) as the same, persistent nubbin. This would imply that the second mAP spigot of the fifth instar is lost in the adult instar without a trace, and would therefore propose yet a third method of spigot or fusule renewal. We prefer to think that the nubbin in the adult instar is the scar of the posterior spigot present in the fifth, because then the overall hypothesis for how spiders renew spinning structures remains (relatively) simple.

A small, presumably non-functional PMS CY spigot is first visible in the fourth instar female (Fig. 9), two molts before maturity in the sixth instar.

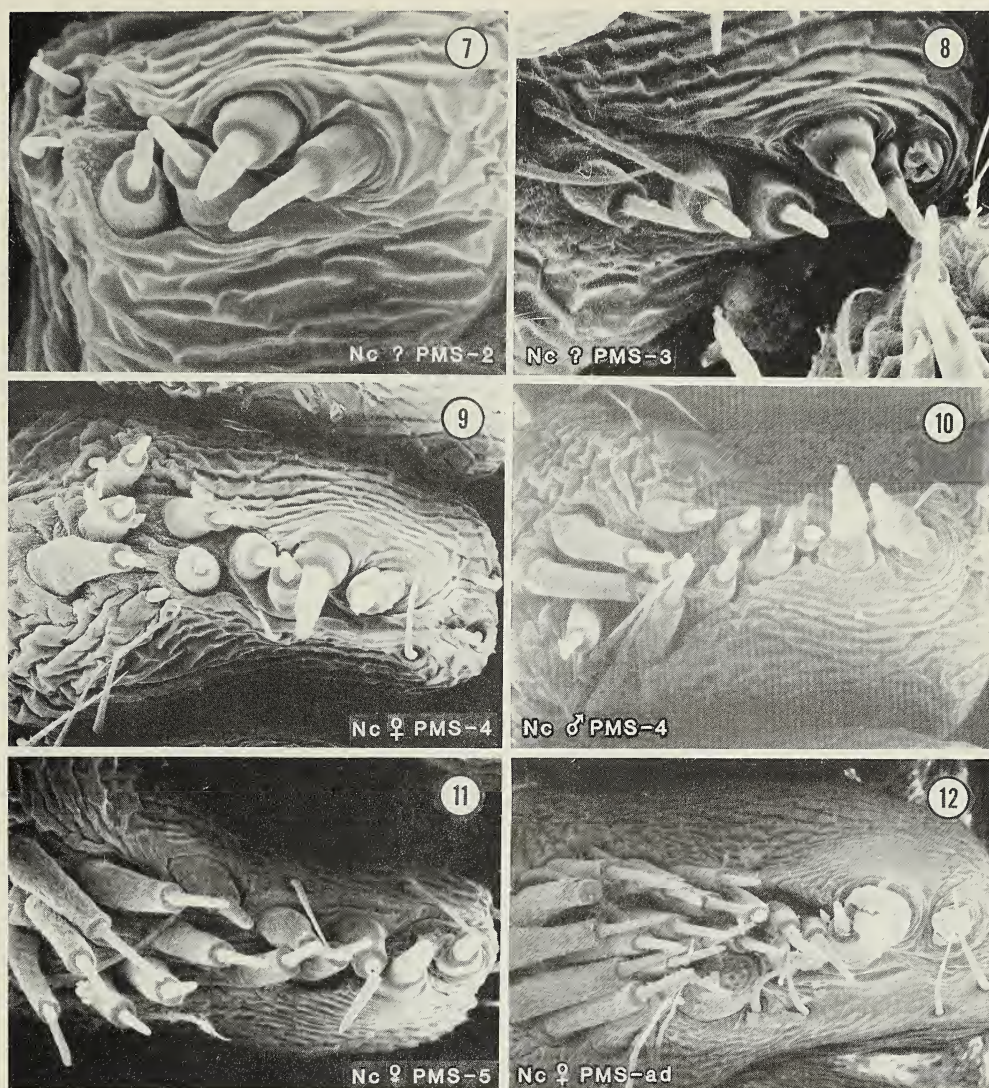
The development of AG and FL spigots is more stable. They also first appear in the second instar (Fig. 13), as usual grouped in a triad. Once present they never atrophy or leave nubbins (except in adult males), and their number remains the same (Figs. 14-18). They are apparently molted *in situ* like any normal



Figures 1-6.—*Nuctenea cornuta* ALS spinneret ontogeny (anterior up): 1, second instar, showing two MAP at left, PI group at right; 2, third instar, note first appearance of tartipores in PI field; 3, fourth instar; 4, fourth instar, male; 5, fifth instar; 6, adult instar, note single MAP spigot and adjacent nubbin.

appendage. They function throughout the ontogeny. Aciniform spigots on the PLS increase in number, and at least from the 4th instar onwards, also show tartipores (Fig. 15-18). Two CY spigots appear in the fourth instar female, two molts before maturity (Figs. 15, 18).

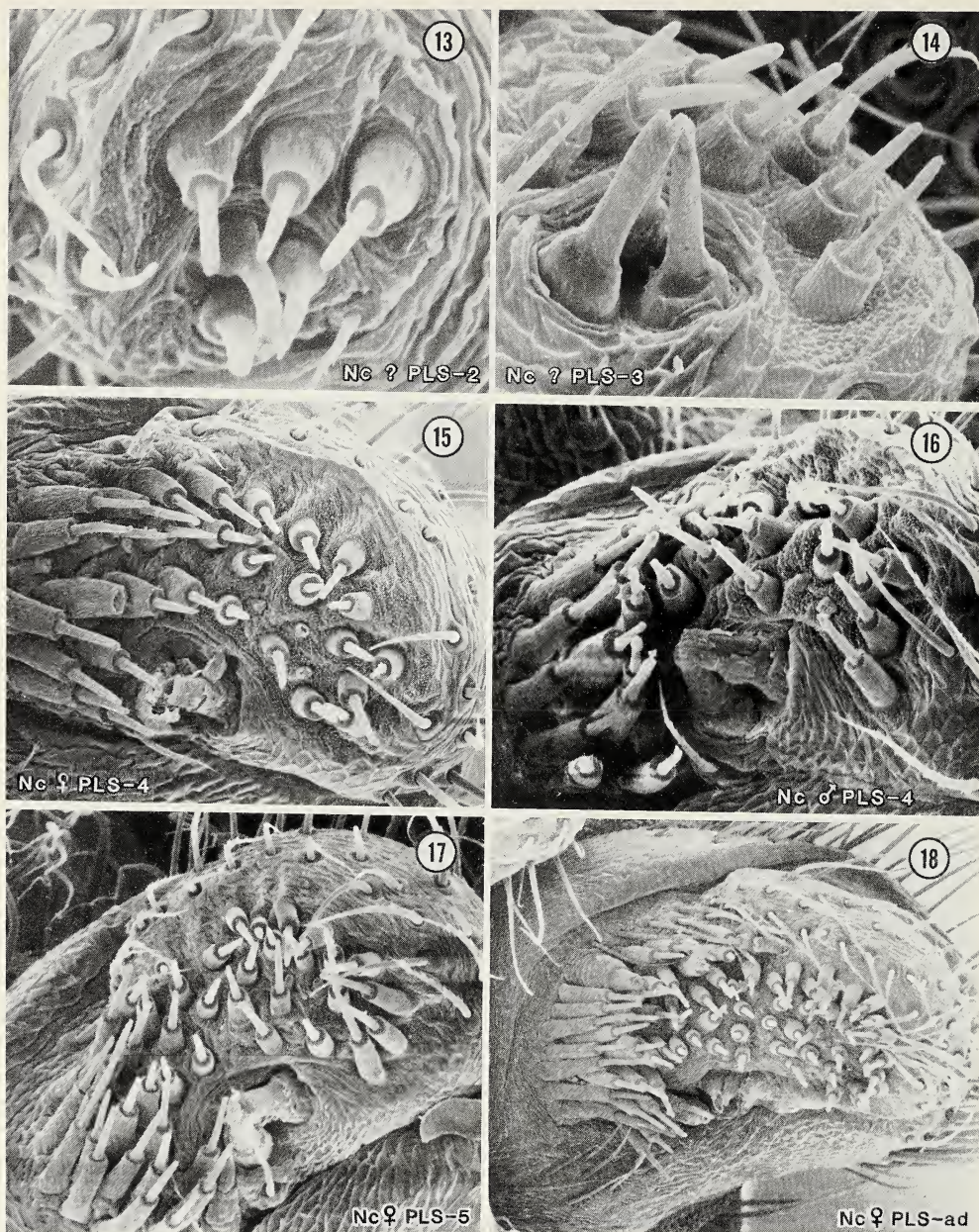
Table 1 shows the number of fusules per spinneret in each instar. Total fusule complement, derived by doubling the counts in Table 1 and neglecting variation



Figures 7-12.—*Nuctenea cornuta* PMS spinneret ontogeny (anterior at left): 7, second instar, showing two mAP at right, two AC at left; 8, third instar, showing two mAP at right with adjacent nubbin, and three AC at left; 9, fourth instar (note appearance of single small CY spigot); 10, fourth instar, male; 11, fifth instar; 12, adult instar, note appearance of mature CY spigot and disappearance of one mAP spigot.

among individuals, is stable in the second instar; 16 ALS piriform, 4 PMS aciniform and 6 PLS aciniform. The variability in the fusule number in 2nd, 3rd, and 4th instars is small and earlier instars show less variation. Fusules on each spinneret increase so that each successive instar has more fusules than the previous one. Excluding the gain from first to second instar, fourth and sixth instars gain relatively more fusules.

One of the two fourth instar specimens examined was male, so that immatures of each sex could be compared as (Figs. 3 and 4; 9 and 10; 15 and 16). Total number of fusules was 172 for the young male and 169 for the young female. Differences in the number of aciniform and piriform fusules in the two sexes are



Figures 13-18.—*Nuctenea cornuta* PLS spinneret ontogeny (anterior up): 13, second instar, showing triad of two AG and one FL spigots below, and three AC spigots above; 14, third instar; 15, fourth instar, note tartipores in AC field and two small CY spigots; 16, fourth instar, male; 17, fifth instar; 18, adult instar, note appearance of two large CY spigots at left.

also small. Evidently males and females do not differ greatly in spinning complements before maturity, although females have CY spigots as early as the fourth instar.

The ontogeny of ALS piriform fusules is special. From the third instar onward, tartipores are found near normal piriforms. The form of the tartipores roughly resembles the vestigial trace left by the lost MAP spigots (Figs. 2-6, 36). We

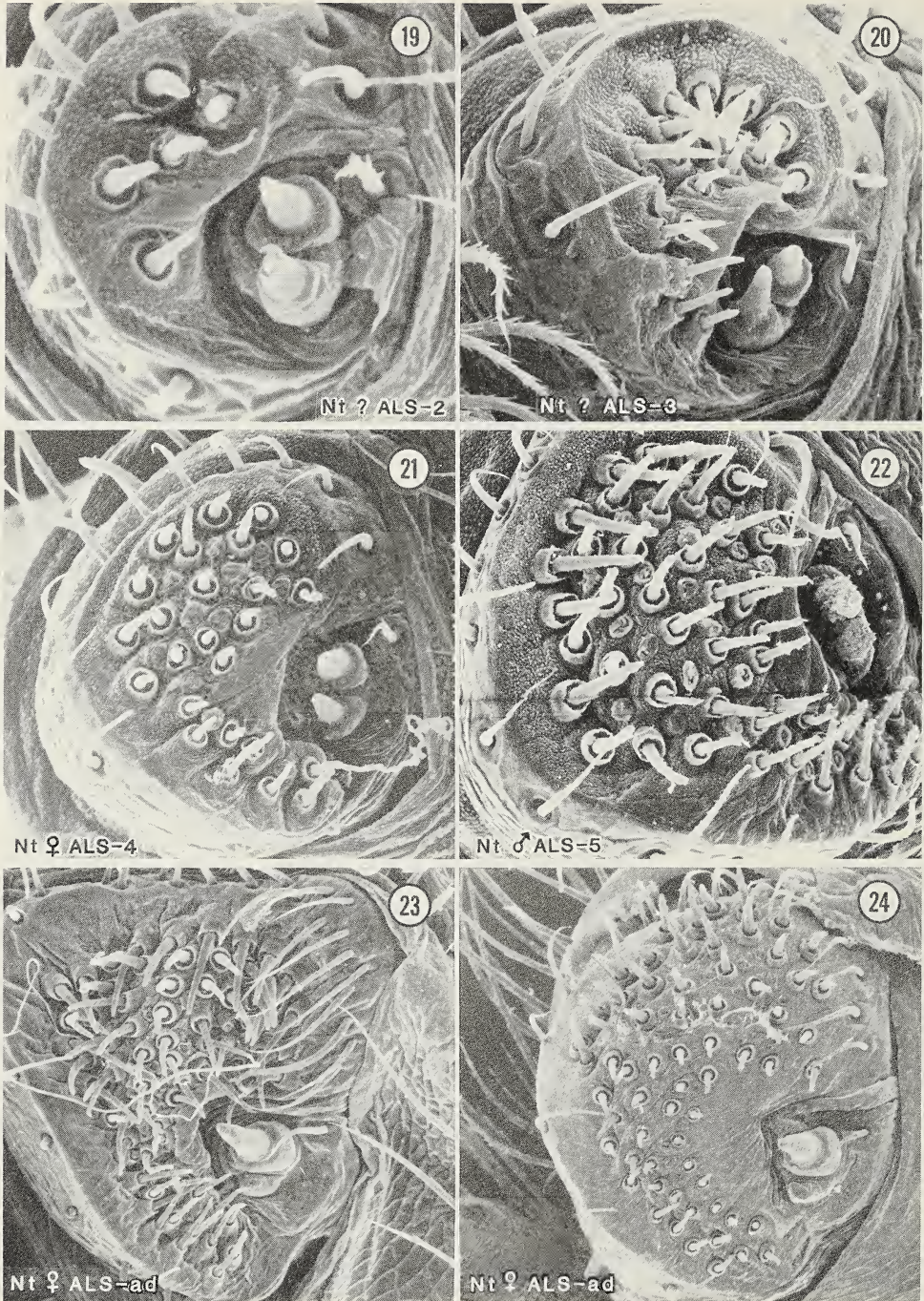
Table 1.—Number of spigots, fusules, and nubbins on each side of the spinning field in each instar of species studied. A range of values reports variation within or among individuals.

	(n)	MAP	mAP	AG	FL	CY	PI	PI tart.	PMS- AC	PLS- AC
<i>N. cornuta</i>										
1st	(15)	0	0	0	0	0	0	0	0	0
2nd	(4)	2	2	2	1	0	8-9	0	2	3
3rd	(4)	2	2	2	1	0	15-17	5-7	6	7-8
4th	(2)	2	2	2	1	3	41,47	20,24	7,10	27,29
5th	(2)	2	2	2	1	3	61,74	26,27	12,15	42,43
6th (adult)	(1)	1	1	2	1	3	110	60	21	59
7th (adult)	(1)	1	1	2	1	3	124	60	20	71
<i>N. theisi</i>										
1st	(4)	?	?	?	?	?	?	?	?	?
2nd	(6)	2	2	2	1	0	5-9	0	2	3
3rd	(4)	2	2	2	1	0	5-17	3-6	4-8	7-13
4th	(3)	2	2	2	1	0	17-31	5-18	10-26	10-23
5th	(3)	—	—	—	—	—	40-45	22-23	42	29-30
6th (adult)	(2)	2	1	2	1	3	58,72	?	59,72	51,57
7th (adult)	(2)	—	—	—	—	—	69,79	?	78	50

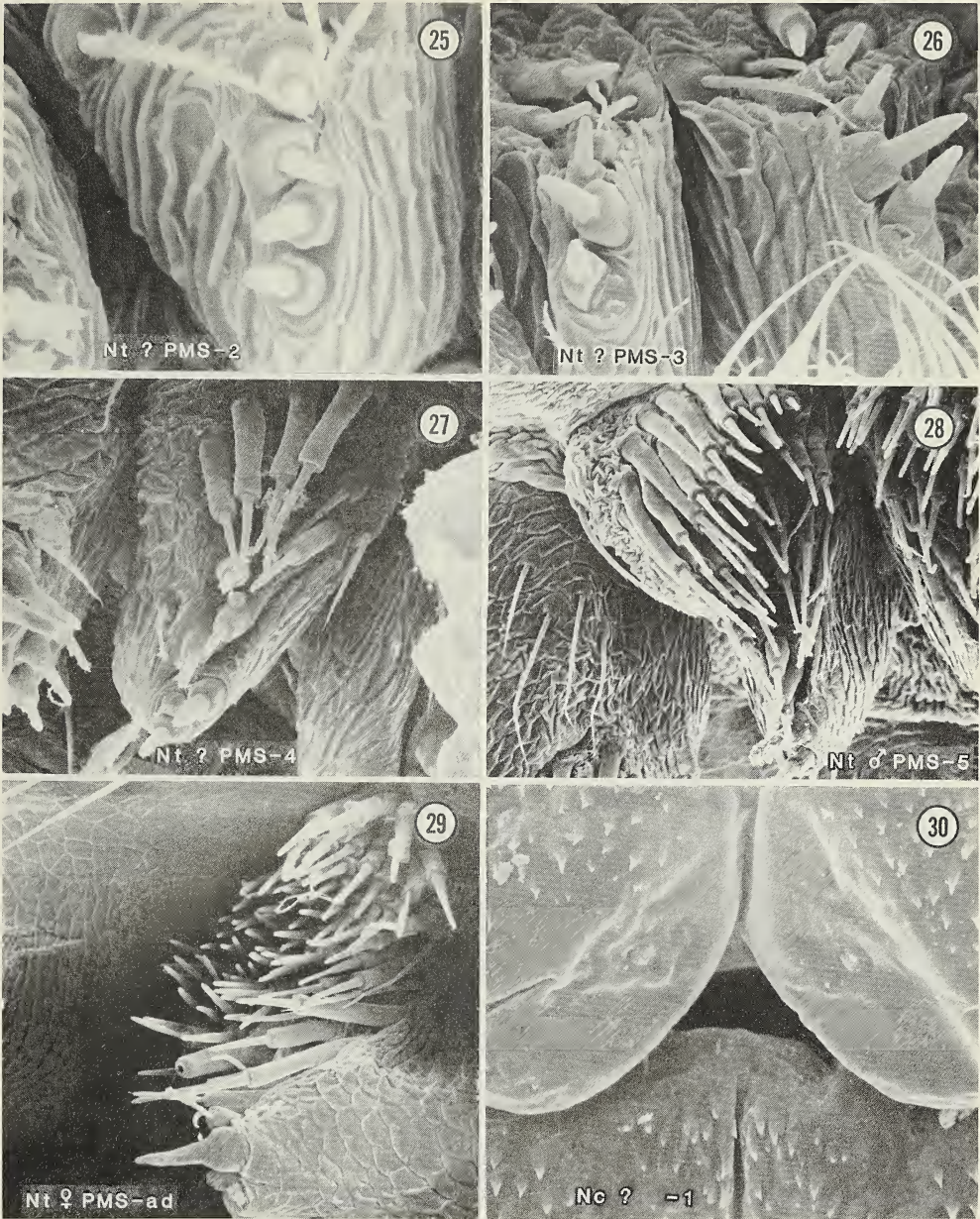
interpret these and other tartipores as vestiges left over from fusules functional in the previous instar. If these tartipores are counted, interesting trends appear (Table 1). In third, fourth and fifth instars, the range of tartipores present in an instar is roughly equivalent to the range of piriform fusules in the previous instar. The second instar PI persist only for this instar because their number (16-18) is roughly equal to the number of tartipores in the third instar (10-14; difference probably due to individual variation). A similar pattern of total replacement probably also occurs in the third instar PI because their number (30-34) roughly equals that of tartipores in fourth instars (40-48). However, we cannot be certain that all fourth instar tartipores can be construed as remnants of third instar PI, because it is possible, although unlikely, that some third instar tartipores persist into the fourth instar. If they do, then some functional third instar PI fusules also persist. The numbers are not exact. Judging from the mAP spigot evidence, however, nubbins themselves can disappear in the course of postembryonic development (the nubbin of the first mAP spigot to atrophy is a example). During young instars therefore, the entire complement of PI fusules may be replaced at each molt.

The development of aciniforms is roughly the same, though not so regular. No tartipores are found in third instars and relatively few are found in subsequent instars. AC fusules apparently function and are molted *in situ* through more molts than PI fusules. Nevertheless, the presence of sparse tartipores from at least the fourth instar on suggests that some AC fusules do atrophy during development, and are "replaced" by new fusules in new positions.

The distribution of ALS and PMS spigots and fusules remains more or less constant during development. The PLS distribution changes the most from third to fourth instars, when the spinneret tip and especially the AC spinning field elongates (Figs. 14, 15). Fourth instar PLS already have the basic topography of the adult.

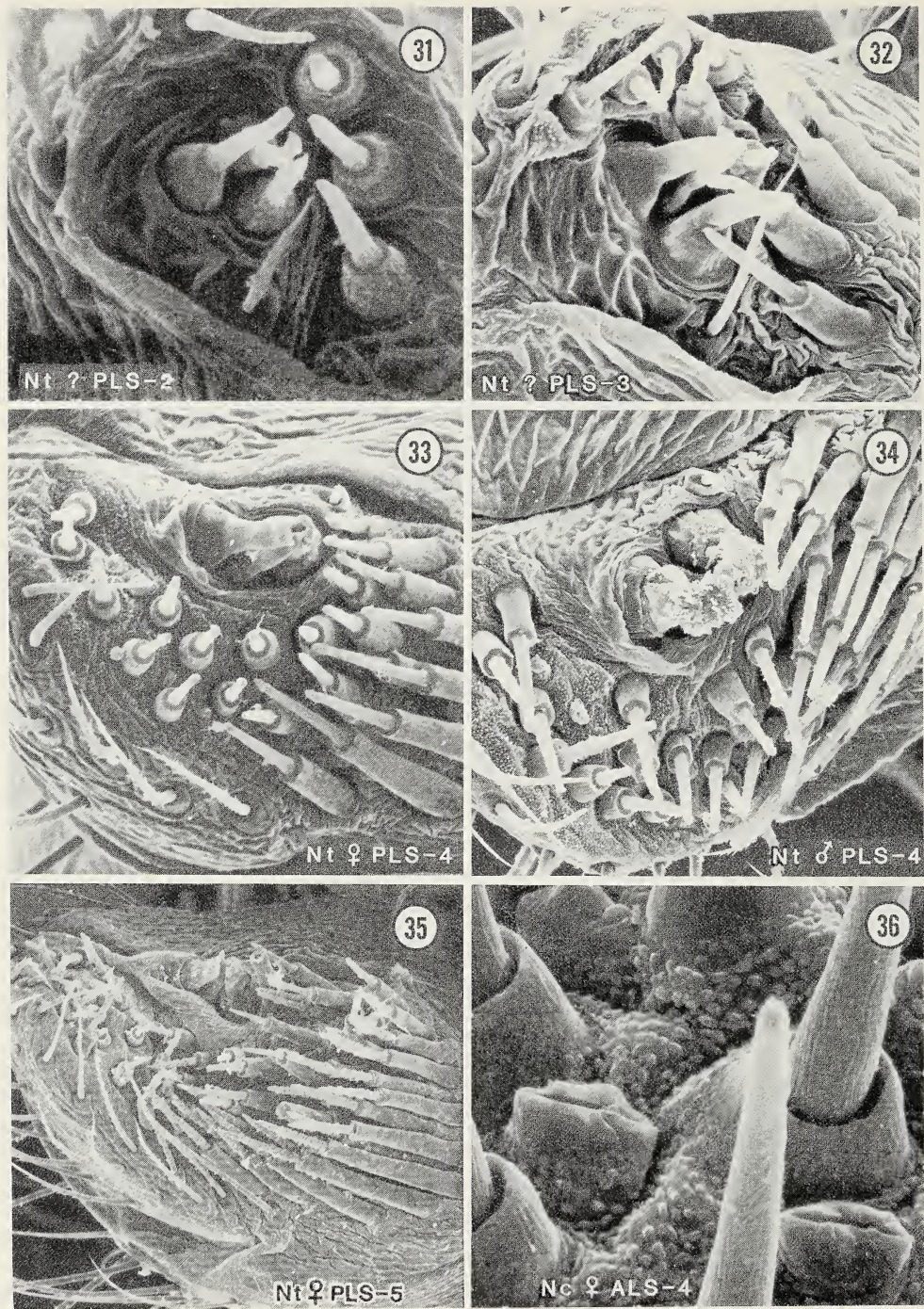


Figures 19-24.—*Neoscona theisi* ALS spinneret ontogeny (anterior up): 19, second instar, showing two MAP at left, PI group at right; 20, third instar; note tartipores in PI field; 21, fourth instar; 22, fifth instar, male; 23, adult instar, note single MAP and adjacent nubbin; 24, adult instar, different individual.



Figures 25-29.—*Neoscona theisi* PMS spinneret ontogeny (anterior up): 25, second instar, showing two mAP below, two AC above; 26, third instar, showing two mAP below with adjacent nubbin, and four AC above; 27, fourth instar; 28, fifth instar, male; 29, adult, note appearance of single CY spigot and disappearance of one mAP spigot.

Figure 30.—Spinning field of first instar *Nuctenea cornuta*, note rudimentary morphology of spinnerets and absence of functional spigots.



Figures 31-35.—*Neoscona theisi* PLS spinneret ontogeny (anterior to the left): 31, second instar, showing triad of two AG and one FL spigots at left, and three AC spigots at right; 32, third instar; 33, fourth instar, note tartipores in AC field; 34, fourth instar, male; 35, fifth instar.

Figure 36.—Closeup of *Nuctenea cornuta* fourth instar ALS, showing tartipores of pyriform fusules.

Neoscona theisi.—The basic pattern of postembryonic growth of spinning structures in this species is similar to *N. cornuta*, and so we only note features that seem particularly significant. However, we illustrate *N. theisi* comprehensively to emphasize that the patterns hold across these genera (Figs. 19-23; 25-35). This consistency argues that individual variation or interspecific variation is unimportant at the level at which we are comparing patterns.

Again, spigots probably first appear in the second instar (Figs. 19, 25, 31). Although all our preparations of first instars failed, this can be inferred from the few spinning structures in second instars, a condition similar to second instar *N. cornuta* (compare Figs. 1 and 19; 7 and 25; 13 and 31, numbers in Table 1).

Adult specimens have one MAP spigot and one mAP spigot with accompanying nubbins as in *N. cornuta* (Figs. 23, 24, 29). One mAP spigot of the second instar also atrophies by the third instar (Fig. 26). The same pattern may occur in the ALS MAP spigot as well in *N. theisi*. If the ALS MAP area in third instars is carefully examined, one possible nubbin can be observed at the inner margin of the posterior MAP spigot (Fig. 20). Like the nubbin near third instar PMS mAP spigot, this appears to be an atrophied MAP spigot which only functioned during the second instar. From the MAP spigot distribution in second and third instars we infer that the third instar posterior MAP spigot is new, and so the nubbin came from the posterior MAP spigot in the second instar. This new MAP spigot also atrophies by the sixth instar. Evidence for a similar process of ALS MAP spigot replacement in third instars of *N. cornuta* is negative or equivocal (Fig. 2).

Fusule number varies more within an instar in this species than in *N. cornuta*. The instar in which the largest number of fusules is gained is difficult to determine, because fusule number seems to increase evenly in each instar.

As in *N. cornuta*, the number of fusules in a fourth instar male and female are very similar (Figs. 33, 34). The same holds true for other spinnerets (male, Figs. 22, 28; female not illustrated). Unlike *N. cornuta*, *N. theisi* fourth and fifth instar females lack rudimentary CY spigots (Figs. 27, 33, 35).

Third instars have many ALS tartipores (Table 1 and Fig. 20). The number of tartipores counted for *N. theisi* is not as accurate as that for *N. cornuta* because piriforms in this species are too densely packed. Tartipores in third and fourth instars can still be easily counted. In Table 1 tartipore numbers in one instar match better fusule numbers in the previous instar than in *N. cornuta*.

The development of the shapes of spinning fields in *N. theisi* is almost the same as that in *N. cornuta* except that the inner margin of the PLS of *N. theisi* are more depressed and it is more difficult to see the whole spinning PLS field. The biggest difference between the adults of the two species is PMS AC fusule number. In *N. cornuta*, the PMS have the fewest fusules among three pairs of the spinnerets, totalling only about 45 (Fig. 12). But *N. theisi* PMS AC fusules total about 150 (Fig. 29).

DISCUSSION

The evidence presented here suggests two different modes in which these species of spiders rejuvenate their spinning fields from one molt to the next. First, spigots and or fusules can be simply molted *in situ*. Presumably these structures are

replaced in the same way that spiders replace their exoskeleton with its associated structures.

Second, an existing fusule or spigot may disappear from one instar to the next, leaving behind a scar of the old spigot or fusule base (either tartipore or nubbin). In the case of spigots, this mode of jettisoning old structures seems usually to be accompanied by the appearance of a new spigot adjacent to the scar. This may also be consistently the case for fusules, but the evidence is strong only for the earliest instars.

Flagelliform and aggregate spigots may be unique in being rejuvenated exclusively by the first mode. Piriform fusules in the third instar, and perhaps subsequently, may be rejuvenated exclusively by the second mode. Aciniform fusules, minor ampullate spigots, and perhaps the primary major ampullate spigot apparently undergo both modes of replacement during their functional lives.

The appearance of CY spigots in *N. cornuta* two instars before maturity is startling, as CY spigots typically appear only in adults (Kovoor 1987). We found no trace of these spigots in *N. theisi* before the adult molt. Perhaps *Nuctenea* is phylogenetically derived in this respect.

Because we did not attempt to describe the spinning complement of an individual through successive molts but instead compared cohorts of individuals from the same eggsac, the variation between individuals weakens the evidence for some of these inferences. We can not be sure that piriforms fail to persist from one molt to the next, or that major ampullates are routinely replaced by the second mode, i.e., the production of nubbins. Many spigots, as opposed to fusules, do persist from one molt to the next.

Our interpretations also depend on the inference that the nubbins and tartipores are in fact vestigial. To some extent, we are merely extending the accepted explanation for spigot nubbins, at least in the case of the ALS major ampullate spigot, to explain structures associated with fusules. These structures have also been interpreted as sensory organs ("petits organes vraisemblables sensoriels," Kovoor 1986, p. 19). Similar structures have been found in most families of spiders excepting mesotheles (Shear et al. 1989). Our interpretation of the PI and AC tartipores as vestigial scars of previous fusules is new. Sectioning of the structures might decide the issue if one assumes that the enervation and secretory connection to the old spigot should also be vestigial, if not absent altogether. Because we did not section nubbins or tartipores, we cannot comment on a possibly sensory role. Evidence at the cellular level on how the molting process affects silk glands is also lacking.

If our inferences are correct, the second mode of renewal would seem to make continuity of silk production through the molting process difficult. Appearance of nubbins or tartipores implies either that the silk gland and duct serving that structure also atrophies, or that the spider somehow connects the old system to the new spigot or fusule in a rather short time. It would be interesting to know if spiders cease using their piriform or aciniform glands in advance of a molt, and if so, how long before. Which spigots make molting cells or chambers? If spiders do switch the connection of ducts at the time of the molt, the process must be complex. The other explanation—that they replace substantial numbers of secretory systems at each molt—also seems somewhat bizarre.

In *N. theisi* and possibly *N. cornuta* one pair of MAP appears to atrophy in the third instar, and another pair appears to compensate for the absent spigot,

thus restoring the status quo for juvenile araneoids. Replacement of one ALS MAP spigot by another in juvenile instars has not been reported previously in araneoid spiders.

Replacement of the ALS ampullate spigot in the third instar is rendered more plausible by the obvious replacement of the ampullate that takes place on the PMS. The ontogenetic patterns are similar. Surprisingly, three pairs of mAP appear during development: two appear in the second instar and one at the third. Two of these disappear before the adult stage. New spigots always seem to emerge posterior to existing ones. This pattern may have been misunderstood by Wasowska (1977) who reported that only one pair of mAP is atrophied before maturity in *Araneus diadematus* Clerck. Perhaps *A. diadematus* shows a different pattern.

Wasowska (1977) reported that spinning structures also appear in the "first" instar in *A. diadematus*, but that AG and FL exist only from the "second" instar; in *Metellina segmentata* (Clerck), spinning structures appear also in "first" instars. Our results agree in part, because Wasowska numbered instars differently, counting the first eclosed stage as first instar, whereas we count it as the second. However, our results also differ in that we found all classes of spinning structures on the second instar. The pattern we found makes more biological sense, because second instars are fully equipped to make viscid catching webs.

The increase in number of PI and AC differs slightly between species. In *N. cornuta* fourth and sixth instars gain the most, but in *N. theisi* the gain between instars is more or less the same. Wasowska (1977) reported that all species studied by her gained the most at the third instar. Our results again differ. Opell (1982) found that the number of fusules in the cribellum of *Hyptiotes cavatus* (Hentz) increased most from the third to fourth, and evenly from the fourth to the sixth instar. This is similar to the ontogeny of *N. theisi*. The gain in number of fusules probably differs between taxa; only more studies will resolve the issue.

Based on the results both from this study and existing papers (Mikulska 1966; Wasowska 1977), all araneid adults examined thus far (and all araneoids) have only one functional pair of ALS MAP spigots, whereas they have two pairs of MAP in some earlier instars. On the other hand, *Metellina segmentata* has two pairs of MAP only in "first" instars; the other four instars have just one pair of MAP (Wasowska 1977). *Metellina segmentata* MAP spigot ontogeny thus seems accelerated relative to the rest of the spinning structures. If true of other tetragnathids, this ontogenetic pattern supports the inference that metines and other tetragnathids are derived araneoids rather than primitive (Coddington 1986, 1989).

The ontogeny of mAP is further evidence for the same inference. According to Wasowska (1977), *Metellina segmentata* and *Enoplognatha ovata* (Clerck) both have just a single mAP during juvenile instars, as opposed to the two mAP characteristic of araneids. By ontogenetic criteria the araneid condition is primitive and thus this evidence confirms both theridiids and tetragnathids as derived ananeoids relative to araneids (Coddington 1989, 1990).

ALS MAP nubbins near the functional MAP are also found in adult uloborids and in *Deinopis* (the latter have numerous ALS MAP). These nubbins apparently reflect MAP existing in younger instars (Coddington 1989). Both deinopoids and araneoids seem to lose the posterior member of the pair. Deinopoids, araneoids

and possibly some dictynids are unique as far as we know in having persistent ALS MAP nubbin(s) in the adult stage (Coddington in press).

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LIFE CYCLE AND BEHAVIOR OF THE KLEPTOPARASITIC SPIDER, *ARGYRODES ULULANS* (ARANEAE, THERIDIIDAE)

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ABSTRACT

This study investigated the life cycle and behavior of *Argyroides ululans* which is a specialist kleptoparasite in the communal webs of its social spider host, *Anelosimus eximius*. Observations of natural and enclosed colonies of *An. eximius* revealed that large *An. eximius* colonies maintain steady populations of high numbers of differently aged *Ar. ululans* individuals whereas small colonies contain fewer kleptoparasites less predictably. Adult female *Ar. ululans* forage almost exclusively by stealing newly captured prey directly from their hosts and were never observed to prey on host spiders. Although male and juvenile *Ar. ululans* will sometimes steal prey from *An. eximius*, they tend to scavenge more and feed on prey scraps abandoned by their hosts.

INTRODUCTION

Spiders in the genus *Argyroides* conduct nearly all of their activities in the webs of other spiders rather than building webs of their own (Exline and Levi 1962; Gertsch 1979). *Argyroides* can exist in a variety of relationships with their host spiders (as commensals, kleptoparasites, predators) depending on factors such as relative size of host and *Argyroides*, morphology of host web, and host feeding rate (Wise 1982; Larcher and Wise 1985). Although specific relationships for certain *Argyroides*-host systems have been determined (Exline and Levi 1962; Smith Trail 1980; Tanaka 1984; Larcher and Wise 1985), the life cycle and foraging behavior of only a few *Argyroides* species have been studied in any detail (Vollrath 1979, 1987; Larcher and Wise 1985; Whitehouse 1986).

Argyroides ululans Cambridge is a specialist kleptoparasite in the communal webs of its host, *Anelosimus eximius* Simon, which lives in the undergrowth of tropical rainforests in Peru. In this paper I describe some aspects of the natural history and behavior of *Argyroides ululans*, including its relative abundance in *Anelosimus eximius* colonies, general activity, reproductive behavior, and foraging behavior. Comparisons are drawn with other *Argyroides* species that have solitary and/or temperate-zone hosts.

METHODS

This research was conducted in the Tambopata Reserved Zone, 35 km southwest of Puerto Maldonado, Madre de Dios, Peru. The reserve is located

within a region of subtropical moist forest described in detail elsewhere (Erwin 1985).

Anelosimus eximius, a highly social spider, is common in this area. These spiders build large communal webs usually within understory vegetation. The webs consist of a dense bowl-shaped sheet or capture surface from which strands of tangled silk extend upward, sometimes for several meters, to form a barrier. Dead leaves and other debris are incorporated into the bowl of the web as retreats. The barrier is less visible to insects and is used to ensnare prey. Colonies at Tambopata average $68.86 \text{ cm} \pm 50.28 \text{ cm}$ (range 10-290 cm) in length (the longest dimension of the three-dimensional bowl) and contain from 5 to approximately 2,500 spiders (Rypstra, unpublished data), most of which are female as in other colonies of this species (Aviles 1986; Vollrath 1986). *Anelosimus eximius* individuals cooperate in prey capture, feeding, colony construction, web maintenance, and care of young (Christenson 1984; Vollrath and Rohde-Arndt 1983).

The barrier webbing of *An. eximius* colonies frequently houses a kleptoparasite, *Argyrodes ululans*, that specializes in stealing prey from its social host. *Ar. ululans* spends its entire life cycle within the barrier portion of *An. eximius* webs where it forages, mates, and lays egg sacs.

Surveys of colonies.—*Anelosimus eximius* colony length and the number of *Argyrodes ululans* individuals inhabiting the colonies were determined approximately every month. I recorded the total number of female, male, and juvenile kleptoparasites within each colony. For two of the colonies (#883 and #885), these data were collected every one to two weeks from September 1 to November 10, 1988.

General activity.—The activity of individual kleptoparasites (adult females, adult males, and juveniles) was monitored for periods of 1 to 4 hours between 0600 and 2300 for a total of 125 spider-hours (one spider observed for 1 hour). Approximately 30-40 individual kleptoparasites in six different natural colonies were observed. Data were collected from August 26 to November 10, 1988.

Mating and reproduction.—*Natural colonies:* During observations of general activity and stealing behavior, 19 matings were observed. I recorded the details of the courtship behavior and the duration of copulation. Some life history and reproductive characteristics of four female *Argyrodes ululans* individuals in natural colony #885 were recorded every day from September 1 to November 10, 1988. I recorded the date of molt from penultimate to adult, date first egg sac was laid, date of hatching, and date second egg sac was laid. For each female I recorded daily whether it was in an active state, inactive and gravid, or guarding an egg sac.

Enclosed colonies: Female *Ar. ululans* that had laid egg sacs in enclosed colonies of *An. eximius* (maintained in screened field enclosures, $30 \times 30 \times 30$ cm, for use in other experiments, Cangialosi 1990b) were used for observations of egg sac guarding behavior. Egg sacs were removed from two females in separate cages and the reaction of each female was recorded. For one of the females, an egg sac of a different female was placed in the cage with her 30 min after the original one had been removed. This was done to see whether the female could recognize her own egg sac and distinguish it from an egg sac of another female.

Foraging behavior.—Detailed observations of the foraging behavior (including prey stealing) of *Ar. ululans* were recorded for adult females, adult males, and

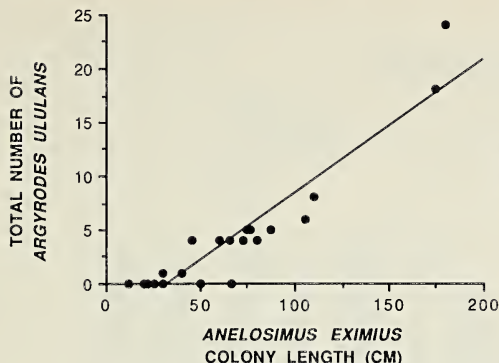


Figure 1.—Linear regression of total number of *Ar. ululans* on *An. eximius* colony length (cm). Equation for the line is $y = -3.99 + 0.124x$; $R^2 = 0.88$.

juveniles foraging in natural colonies of *An. eximius*. Observations were made for both naturally entering insects and those that were introduced purposely by dropping or gently throwing them into the colonies.

RESULTS

Abundance of *Argyrodes ululans*.—Colonies of *An. eximius* contained from zero to 24 individuals of *Ar. ululans*. The number of *Ar. ululans* per colony increases with increasing host colony size (Fig. 1). The relative proportions of females, males, and juveniles that comprise the total population of *Ar. ululans* living within a colony is dependent upon the size of the colony and changes during the course of a season (Fig. 2). In colony #885 (medium sized; 87-93 cm), the number of juveniles decreased steadily from five to zero between September 1 and October 8 and remained at zero until an egg sac hatched on November 5 (Fig. 2a). The number of adult females and males in colony #885 remained constant after the disappearance of the juveniles (from maturation or dispersal). In colony #883, which was larger than #885 (175-188 cm), there was a consistently high number of juveniles and the number of mature females increased from September 1 to November 10 (Fig. 2b). Adult males remained relatively low in comparison to the number of females in this colony.

General activity and behavior.—Eight behavioral activities of *Ar. ululans* were recognized and recorded: (1) rotary probing (rotating the first pair of legs at the coxatrochanter joint, Cangialosi 1990a); (2) feeding (extracting food from prey); (3) folded (resting or inactive position in which the spider remains motionless in the web with the legs folded up near the body, Fig. 3a); (4) still (also an inactive state in which the spider sits in the web motionless with the legs outstretched, Fig. 3b); (5) grooming (cleaning legs by passing them through the chelicerae); (6) mating (courtship and copulation); (7) stealing behaviors (including leg waving, web shaking, and clearing silk); and (8) walking (locomotion on the webbing).

Overall, the proportion of time allocated to the different categories of behavior is not independent of the time of day for adult females (3×8 contingency table, $\chi^2 = 80.78$, $P < 0.001$), adult males (3×7 contingency table, $\chi^2 = 48.13$, $P < 0.001$) or juveniles (3×7 contingency table, $\chi^2 = 140.98$, $P < 0.001$). Females are more likely to be in a folded rest state from 0600 to 1100 hours, feeding from 1101 to 1600, and in a still position from 1601 to 2300 (Fig. 4a). Males spend most of their time in a still position but are less likely to do so from 0600 to 1100

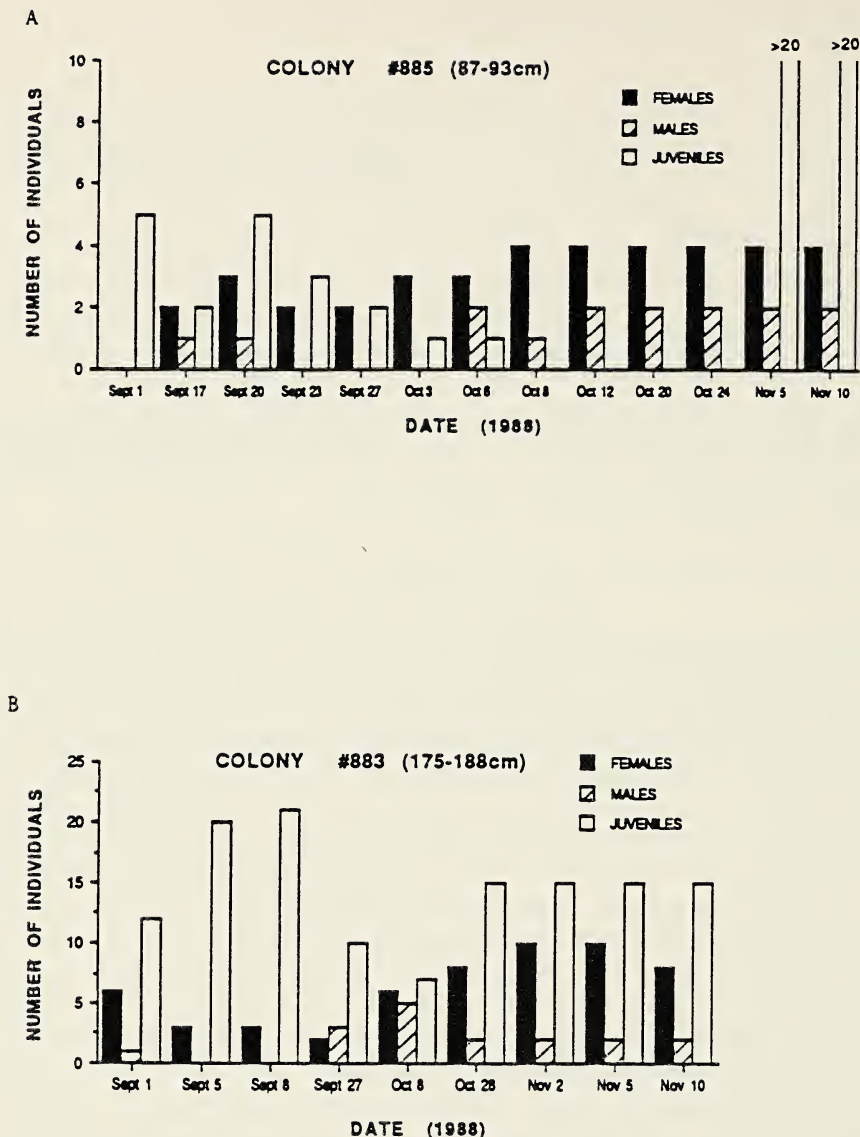


Figure 2.—Total number of female, male, and juvenile *Ar. ululans* in *An. eximius* colonies for dates in Sept and Nov, 1988. A, colony #885 (87-93 cm); B, colony #883 (175-180 cm).

(Fig. 4b). Rotary probing for males is more common from 0600 to 1100 and from 1601 to 2300 (Fig. 4b). No adult males were observed feeding during these observations. For juveniles, a folded rest state is more likely from 0600 to 1100 and a still position is more common later in the day (Fig. 4c). Similar to adult females, juveniles also spend most of their time feeding from 1101 to 1600 (Fig. 4c).

Mating and reproduction.—Compared to many other spider species, the courtship behavior of *Ar. ululans* is relatively short and simple. Within the barrier webbing of the *An. eximius* colony, a rotary probing male slowly approaches a female until he almost contacts her. Unreceptive females drop or walk away from the male. A receptive female also begins to rotary probe directly facing the male. After just a few seconds, copulation commences and continues

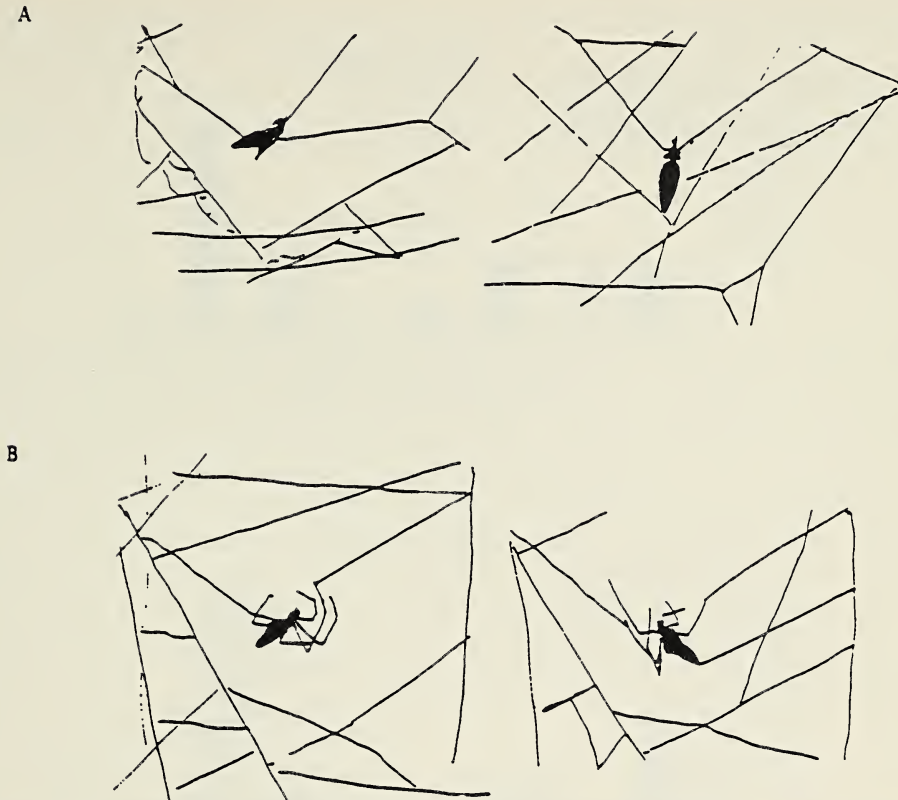


Figure 3.—Diagrams of rest positions of *Ar. ululans* in *An. eximius* webbing. A, legs folded against body, B, legs outstretched. (Drawings by Rebecca Ellis).

from 2 to 15 min ($N = 19$) until the pair breaks apart and the spiders resume other activities. After separating, two of the males observed approached another female and also mated with her.

The females observed in colony #885 took from 14 to 19 days to lay their first egg sac after reaching maturity (Table 1). One of the females produced a second egg sac 12 days after the first (Table 1). Two to four days before laying eggs, gravid females assume an inactive folded position high in the *An. eximius* colony barrier and do not forage. An adult female *Ar. ululans* suspends its egg case in the barrier web at night and guards it until hatching. A guarding female spends almost all of her time in a folded position near the egg sac. When it is threatened by another spider or an insect approaching nearby, it becomes alert and shakes the web and egg sac sharply, which causes the intruder to flee. Guarding females only stray away from their egg sacs in order to drink water from the silk strands within a 5-10 cm radius around the egg sac; they do not forage or feed. The guarding/hatching time for three of the females in colony #885 was 17 to 18 days (Table 1). Mean hatching time (time since egg sac is first laid until the young emerge; not guarded since females were removed from egg sacs placed in vials) for egg sacs laid in the cages was 22.8 days ($SD = 2.32$, $N = 6$, range 20-27).

Female *Ar. ululans* with egg sacs become active foragers only if the egg sac is lost, or after the egg sac hatches. Female #3 in natural colony #885 lost its egg sac 6 days after laying (cause unknown) and resumed foraging that same day.

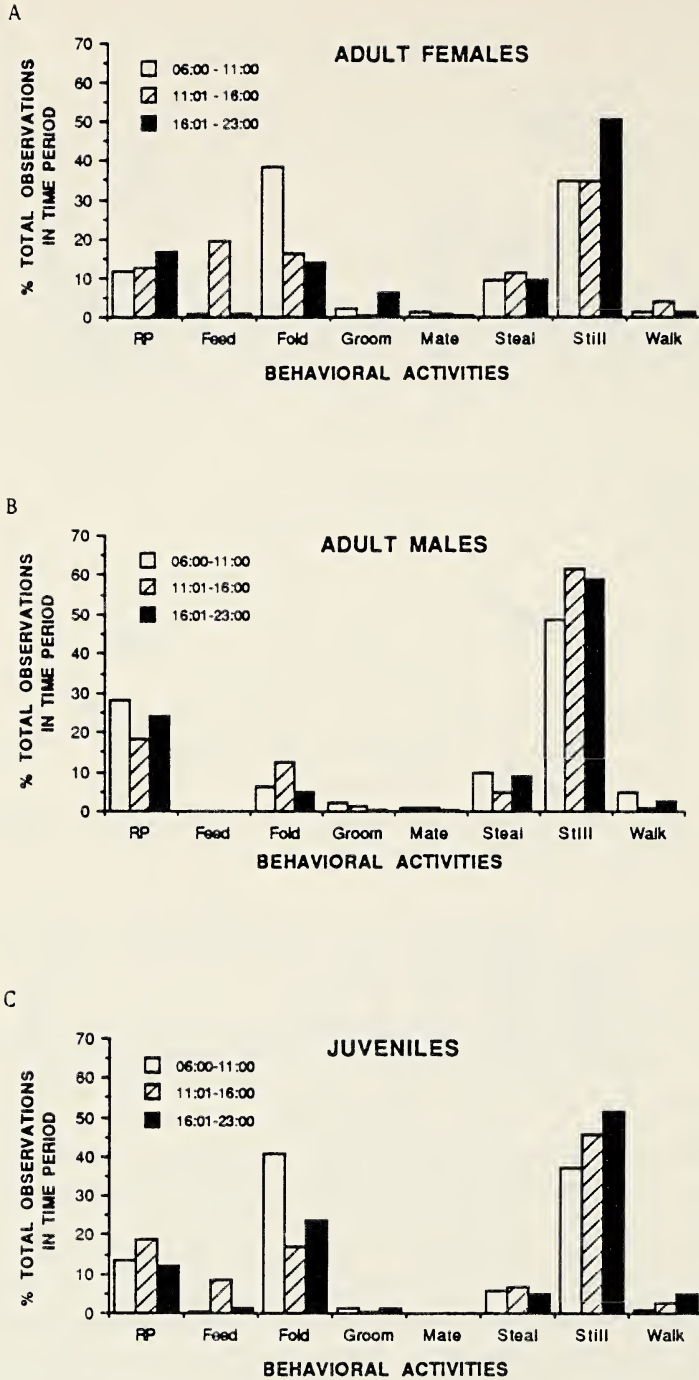


Figure 4.—General activity of *Ar. ululans*. Percentage of total observations of different behavioral activities in three time periods, 0600-1100, 1101-1600, 1601-2300. RP = rotary probing; Feed = feeding; Fold = folded position; Groom = grooming; Mate = mating; Steal = web shaking, silk clearing, and leg waving; Still = still position; Walk = walking. A, adult females, B, adult males, C, juveniles.

Table 1.—Some life history characteristics for four female *Ar. ululans* individuals. Time units are days. (a = egg sac lost).

Female	Penultimate to adult	Maturation molt to 1st egg sac	Guarding time (hatching time)	Time to 2nd egg sac
1	—	—	17	12
2	16	15	18	—
3	—	19	6 ^a	29
4	16	14	18	—

After removing an egg sac from its owner (which was laid in a cage 3 days earlier), the female immediately started to search for the egg sac, wandering around the area rotary probing and moving further and further away from its original position for 105 min until she became inactive (folded). This female did not attempt to steal prey that day or the following day, but was successful in stealing a prey item two days after the egg sac had been removed. Removing an egg sac from a second female in another cage produced similar searching behavior. For this second female, an egg sac laid by a different female was placed in the cage in the vicinity of the original egg sac after 30 min of searching. The female investigated the egg sac for 5 min, moving around it and touching it with her first pair of legs. She then became inactive and folded near the egg sac. By the next day, this female had attached this new egg sac to the colony webbing and was guarding it in the usual way.

Foraging behavior.—*Females:* *Ar. ululans* females feed primarily by stealing prey freshly captured by its host. It specializes in *An. eximius* webs as it was never found in webs of any other spider species examined on the study site including all located colonies (8 total) of two other *Anelosimus* species (pers. observ.). A Peruvian arachnologist involved in making a comprehensive collection of the spider fauna at the site examined virtually every spider web that could be located for a month in 1987 and a month in 1988. This investigator found no *Ar. ululans* in any of the spider webs (other than *An. eximius*) that she examined (D. Silva pers. comm.).

The main sequence of events for stealing attempts by adult females is summarized in Fig. 5. (The individual behaviors of the kleptoparasites and of *An. eximius* are described in more detail in Cangialosi 1990a and Cangialosi 1990b). A female *Ar. ululans* locates a prey item in the process of being captured by *An. eximius* by detecting vibrations while rotary probing. The kleptoparasite approaches the prey slowly and waits above it (10–15 cm) in a still position until the prey is subdued by the social spiders. Once the prey is immobilized, the kleptoparasite moves more quickly toward it, either leg waving or clearing silk, and then starts web shaking. The relative frequency of these behaviors varies depending on such factors as the number of host spiders involved and their reaction (Cangialosi 1990a). Once the prey item is cleared of host spiders, the kleptoparasite attaches the prey to itself via a silk line, and transports it up into the barrier web to feed. Females were never observed killing an *An. eximius* individual but were observed feeding on them on five occasions (two adult females, one adult male, one juvenile) in natural colonies. In the cages, the host spiders that were observed eaten by kleptoparasites were those that were accidentally killed from prey movements during prey capture ($N = 3$).

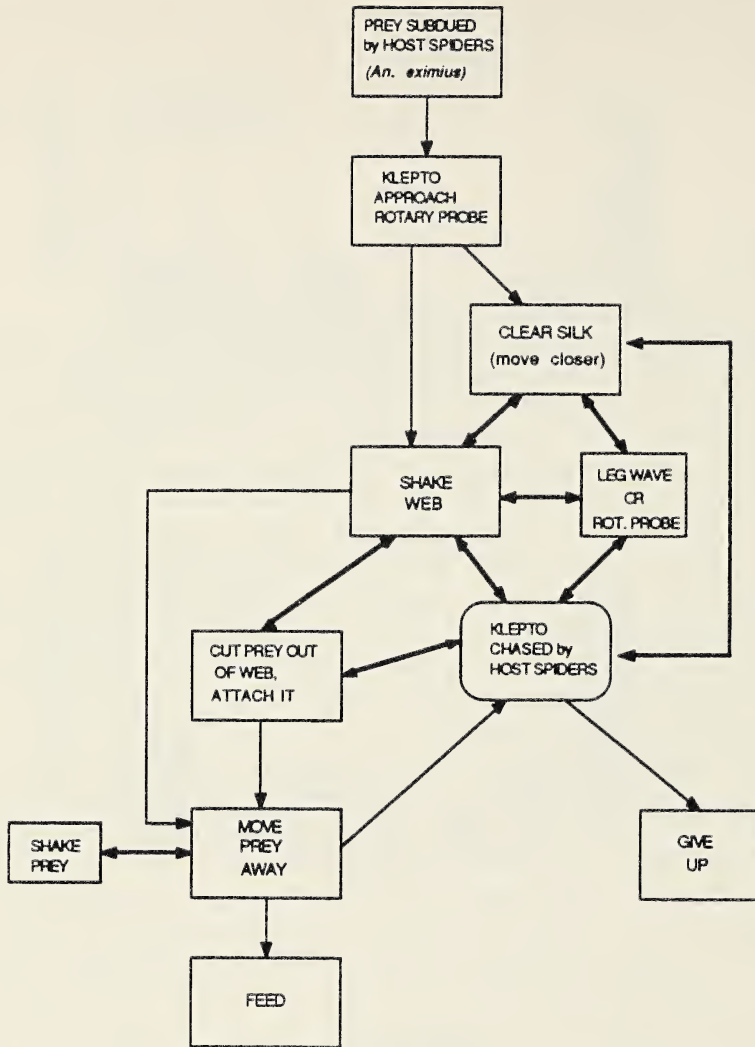


Figure 5.—Ethogram of adult female *Ar. ululans* prey-stealing behavioral sequences.

Males: Adult males spend very little time feeding (Fig. 3). However, males were observed attempting to steal prey six times in natural colonies. Males tend to scavenge more, feeding on prey left in the web by the social spiders and do not usually transport prey. Insects or pieces of insects that have been in the webs for several hours have only a few (if any) host spiders still feeding on them. The kleptoparasite may shake the web and prey to remove these hosts and then feed on the prey without transporting it.

Juveniles: Younger juveniles of both sexes tend to forage similarly to adult males. However, in addition to scavenging for abandoned prey, they sometimes move in and feed with the host spiders on newly captured insects. The hosts apparently do not detect these kleptoparasites since they are able to feed for long periods of time. As they get older, female juveniles begin to behave more and more like adult females and exhibit the same stealing behaviors. Even relatively small, immature kleptoparasites can remove host spiders from prey by web shaking.

No *Ar. ululans* (of any age or sex) were observed capturing even the smallest prey on their own. In fact, when an *Ar. ululans* individual approaches and touches a still insect that begins to move when contacted, the kleptoparasite will back away from it quickly. This sometimes alerts the host to the insect's presence and they will attempt to subdue it. Afterwards, the kleptoparasite may try to steal the newly captured prey.

DISCUSSION

Abundance and age/sex structure.—Large colonies of *Anelosimus eximius* harbor greater numbers of *Argyrodes ululans* than small colonies. Smith Trail (1980) found a higher number of *Argyrodes ficitilium* (Hentz) and *Ar. baboquivari* Exline and Levi in communal groups of *Philoponella oweni* (Chamberlin) compared to solitary *P. oweni*, and no more than one *Argyrodes* was ever found in any solitary web. She presents evidence that suggests that this distribution is due to the fact that *Argyrodes* encounter communal groups more often than solitary webs, and that *Argyrodes* remain longer in communal groups, which probably represent a large source of potential prey to these predatory species of *Argyrodes*. Elgar (1989) found a significant positive correlation between aggregation size of the orb-weaver, *Nephila edulis* Koch and the number of kleptoparasites, *Ar. antipodanus* Cambridge per web (after correcting for *N. edulis* body size). He demonstrated that spiders in aggregations suffered a higher colonization rate of kleptoparasites than spiders in solitary webs, which could explain the kleptoparasite distribution. However, webs of other solitary host species often contain many *Argyrodes* individuals (Robinson and Robinson 1973; Rypstra 1981; Wise 1982; Larcher and Wise 1985).

Although larger colonies of *An. eximius* may have higher kleptoparasite immigration rates, the fact that *Ar. ululans* completes its entire life cycle within host colonies means that new kleptoparasites are added as the older ones reproduce. Larger stable colonies are inhabited by a greater number of kleptoparasites of all ages and reproductive states, and kleptoparasite spiderlings hatch from egg sacs fairly regularly. Hence, the proportion of juveniles in large *An. eximius* colonies stays relatively constant over time, thus maintaining a steady supply of kleptoparasites. In smaller colonies, which might contain a few adult females for only a certain time period, the hatching of juveniles is more sporadic. Thus the presence of kleptoparasites in these colonies is less consistent. Several smaller to medium sized colonies (12-65 cm) often contain no *Ar. ululans* at all.

Although some *Ar. ululans* offspring remain in the natal colony, many newly hatched spiderlings disappear shortly (1-2 days) after emerging. Presumably, some percentage of these aurally disperse to other colonies. It is unclear how random dispersal results in the location of new host colonies. Older juveniles and adult males also occasionally show up in colonies that previously contained no kleptoparasites. The mechanisms, frequency, and patterns of emmigration require further investigation.

General activity.—Most spider species are predominately active either diurnally or nocturnally but not both (Foelix 1982). *Ar. ululans* forages in both the day and night and rests intermittently. The activity of this kleptoparasite, not

surprisingly, appears to be generally geared to its host which, unlike most spider species, actively forages 24 hours a day (Rypstra unpublished data; pers. observ.). *Ar. elevatus* is day-active and *Ar. caudatus* is night-active when they cohabit *Nephila clavipes* webs (Vollrath 1976). Being active at different times, along with other behavioral and physiological adaptations, allows them to exploit their host in different ways (Vollrath 1976, 1987).

Differences in behavioral activity of *Ar. ululans* among the time periods were mainly due to differences in behaviors not related to prey stealing such as changing from a still to a folded position. The significance of these two rest states is ambiguous. The legs-outstretched still position would seem to be more of an alert state than the legs-folded position; however, *Ar. ululans* quickly switches from a folded position to active behaviors when responding to prey. Sex differences in timing of behavior may be related to mating activity. Males spend more time rotary probing (probably in search of mates) when females are less likely to be feeding.

Mating and reproduction.—The mating behavior of *Ar. ululans* is very simple and unritualized. Elaborate courtship displays by male spiders generally function to suppress the females' predatory behavior toward the males (Bristowe and Locket 1926; Platnick 1971; Foelix 1982). Because *Ar. ululans* is non-predatory, it is reasonable to assume that the lack of extensive courtship in these kleptoparasites is due to the fact that males are not in danger of being eaten.

The cessation of foraging during egg sac guarding (17-27 days) implies that egg predation pressure is very strong for *Ar. ululans*. Since foraging resumes within hours of an egg sac being lost, it is important for the kleptoparasites to immediately start gaining reserves to produce a new one. To this end, they apparently undergo quick physiological changes from a fasting state (and from relative inactivity) to an active feeding state. Also, the diligent searching behavior for lost egg sacs indicates that female *Ar. ululans* are sensitive to the presence of their egg sacs. This might imply that abandoned egg sacs have little chance of surviving to the hatching stage.

An. eximius cleans its web regularly (pers. observ.; Rypstra pers. comm.; Vollrath and Rohde-Arndt 1983; Christenson 1984) and undoubtedly removes unattended *Ar. ululans* egg sacs from their communal web. In spite of this, there may be benefits for *Ar. ululans* associated with suspending their egg sacs in *An. eximius* colonies. *An. caudatus* (Taczanowski) females place their egg sacs away from host webs and guard them until the young hatch, whereas *Ar. elevatus* (Taczanowski) leaves its egg sacs unattended in host webs (Vollrath 1987). The behavior of the host and the nature of its web may determine, in part, the placement and guarding of *Argyrodes* egg sacs. Additionally, *Ar. elevatus* produces more egg sacs (with more eggs per sac) than *Ar. caudatus* (one every 5 days for *Ar. elevatus* compared to one every 30 days for *Ar. caudatus*, Vollrath 1987). Vollrath (1987) suggests that, because of these and other factors, *Ar. elevatus* is a more 'r-selected' species whereas *Ar. caudatus* is a more 'K-selected' species (Pianka 1970). In these respects (low egg sac output and tenacious guarding), *Ar. ululans* is more similar to *Ar. caudatus*. This might indicate that *Ar. ululans* also tends to be more 'K-selected', however other factors such as generation time and mortality need to be considered.

Foraging behavior.—*Ar. ululans* is a host-specific kleptoparasite which takes a substantial portion of its hosts' prey (Cangialosi in press). Males and juveniles

tend to scavenge more and perhaps function as commensals rather than kleptoparasites. Juvenile females switch to stealing newly captured prey directly from their hosts as they age and therefore turn more kleptoparasitic.

Wise (1982) suggested that predation may be more important for temperate *Argyroides* whereas kleptoparasitism might be more important for tropical *Argyroides*. This conclusion was based mainly on the fact that most tropical host spiders studied are large orb-weavers (Robinson and Robinson 1973; Rypstra 1981; Vollrath 1979) and that kleptoparasitism is more likely when the *Argyroides* is much smaller than its host, and predation is more likely when *Argyroides* is bigger than its host. The temperate *Argyroides* species studied by Smith Trail (1980) are large compared to their hosts and are primarily predators. Individual adult female *Ar. ululans* and *An. eximius* are roughly equivalent in body size (5-9 mm) and adult *Ar. ululans* are bigger than *An. eximius* juveniles (subordinate). Nonetheless, *Ar. ululans* appears to be nearly exclusively kleptoparasitic. Because it is social, groups of *An. eximius* make this host "bigger" than *Ar. ululans* (and therefore defensively stronger, Cangialosi, 1990b) making kleptoparasitism more likely than predation.

Although direct predation by *Ar. ululans* on *An. eximius* individuals was not observed (even for individuals starved six days, Cangialosi 1990a), *Ar. ululans* were occasionally observed feeding on their hosts. These may have been individuals that were already dead and scavenged by the kleptoparasites. Other *Argyroides* species have been observed to kill and/or feed on *An. eximius* (Rypstra, unpublished data; Vollrath 1982). Tanaka (1984) found that *Argyroides fissifrons* O. P.-Cambridge (which is much smaller than its hosts) preys on its hosts when they are molting and therefore motionless. Because *Ar. ululans* does not kill its host, capture its own prey, or cannibalize its mates, it would be interesting to investigate whether they have venom which is capable of immobilizing prey.

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RESEARCH NOTES

PREDATION ON THE GREEN TREEFROG BY THE STAR-BELLIED ORB WEAVER, *ACANTHEPEIRA STELLATA* (ARANEAE, ARANEIDAE)

Treefrogs are generally the predator and not the prey of spiders. McCormick and Polis (1982) listed three instances of in which the reverse was true: a funnel-web mygalomorph, *Atrax formidabilis* Rainbow; the araneid *Nephila clavipes* (L.); and a pisaurid, *Dolomedes okefenokensis* Bishop.

On 12 August 1989 at ca. 0830 hours, I observed a female star-bellied orb weaver spider, *Acanthepeira stellata* Walckenaer, feeding on the remains of a green treefrog, *Hyla cinerea*. The predation occurred ca. 1.0 km north north-east of Saucier, Harrison County, Mississippi. The spider was collected, along with its prey, from the remnants of a web which was attached from the top of a pokeweed (*Phytolacca americana*) along a fenceline (ca. 1.5 m above the ground) to an overhanging branch of a live oak (*Quercus virginiana*) which extended over the fence.

The spider was collected while it was feeding upon the right lateral side of the treefrog's abdomen. Both spider and treefrog were preserved in 80% ETOH and deposited in the author's personal collection. Judging by the condition of the treefrog, the capture was probably made during the previous night. The treefrog had received two separate bites. Other than the abdominal feeding punctures, the remaining bite was given to the dorsal area on the right thigh.

Measurements of spider and prey were made within 24 hours of collection. The length of the spider was 15.5 mm. The treefrog measured 3.3 cm from snout to vent. No dry weight was taken. No doubt the nearly two-fold difference in size betwixt predator and prey was compensated by the web and venom of the former.

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SPIDERS (ARANEAE) IN THE DIET OF AMERICAN WOODCOCK IN MAINE

Birds are recognized predators of spiders (Gertsch 1979; Kaston 1981). Although numerous studies have reported spiders in avian diets, most concern passerine species (e.g., Orians and Horn 1969; Cowie and Hinsley 1988; Guinan and Sealy 1987) and few identify spiders to family or generic level. Information on the taxa of spiders consumed by avian species will expand our knowledge of bird-spider and predator-prey interactions.

The American woodcock (*Scolopax minor*) is a ground-dwelling bird that feeds on invertebrates on and beneath the forest floor. Woodcock use their long bill to extract prey from the soil and to capture prey on the surface (Sheldon 1967). Quantitative analyses of woodcock food habits include spiders (Pettingill 1936; Sperry 1940; Miller 1957; Krohn 1970), but the taxa consumed were not identified. These studies also indicate that spiders compose a small percentage of the biomass consumed by woodcock; however, a more recent analysis in Maine suggests that spiders may be more important when the woodcock's primary prey, earthworms (Lumbricidae), are less available (Vander Haegen unpublished data). This note documents the family, genus, and, in some cases, species of spiders consumed by American woodcock collected on the Moosehorn National Wildlife Refuge, Washington County, Maine.

Woodcock were collected from late March - late June, 1987-1989, either by shotgun ($N = 45$), or as incidental mortalities from a radio-telemetry study ($N = 15$). Immediately after shooting, 70% ethanol was forced down the esophagus to retard digestion. Contents of the esophagus, proventriculus, and ventriculus were removed and preserved in 70% ethanol. Contents were later submerged in a shallow dish and examined with a stereomicroscope (10-60X). Spiders and spider parts were removed and identified by the junior author. When genitalia were present, specimens were identified to species based on keys and species descriptions in Kaston (1981) and other consulted sources. In the absence of spider genitalia, most parts could be identified only to order, family, and sometimes genus. All spiders and spider parts were stored in 2-dram vials and will be deposited in the arachnid collections of the U.S. National Museum of Natural History, Washington, D.C.

Fifteen of 60 (25%) woodcock examined contained the remains of from 1 to 3 spiders. Spiders of 4 families, 5 genera, and at least 5 species were identified (Table 1). Hunting spiders outnumbered web-spinning spiders 19 to 2; remains of 3 spiders were undetermined. *Trochosa* was the dominant genus among spider prey found in woodcock digestive tracts. All of the identified genera except *Coras* were also captured during expellant sampling of the sub-litter layer of woodcock feeding habitats on the Refuge (Jennings et al. 1990).

The preponderance of hunting spiders eaten by woodcock was not reflected in the results from expellant sampling, where web-spinning spiders outnumbered hunters 2 to 1 (Jennings et al. 1990). This suggests that woodcock either were encountering a greater percentage of hunting vs. web-spinning spiders, or were better able to detect and capture hunting vs. web-spinning spiders. Many of the web-spinning species collected by expellant were small spiders of the families Theridiidae, Linyphiidae, and Erigonidae. We suspect that such small spiders are

Table 1.—Species and number of spiders found in American woodcock stomachs, Moosehorn National Wildlife Refuge, Washington County, Maine, 1987-89.

Family Species	Number		
	Male	Female	Juv.
Agelenidae			
<i>Cicurina brevis</i> (Emerton)		1	
<i>Coras</i> sp.			1
Lycosidae			
<i>Trochosa terricola</i> Thorell	2	2	
<i>Trochosa</i> sp.	1		11
Clubionidae			
<i>Clubiona canadensis</i> Emerton		1	
<i>Clubiona</i> sp.			1
Thomisidae			
<i>Xysticus</i> sp.			1
Undetermined			3

below the threshold of acceptable prey-size for woodcock. The stomach-content results (Table 1) support this hypothesis because most of the spider prey eaten by woodcock were Lycosidae, which generally are larger than species of theridiids, linyphiids, and erigonids.

All identified genera eaten by woodcock were also captured during pitfall trapping in spruce-fir forests of Maine (Hilburn and Jennings 1988; Jennings et al. 1988). Hunting spiders, predominantly Lycosidae, were abundant in pitfall-trap catches in Maine, a result attributable to the roving nature of this foraging guild (Uetz and Unzicker 1976). The mobility of hunting spiders may also make them more available to foraging woodcock. This study indicates that soil- and litter-inhabiting spiders are included in the diet of American woodcock in Maine.

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IMBIBITION OF PRECIPITATED FOG BY NAMIB DESERT SCORPIONS

The Namib Desert is one of the most arid areas on the planet, annually receiving an average rainfall of 7-64 mm (coast to 110 km inland to the east; Seely 1978). However, sections of the desert within ~50 km of the coast of the Atlantic Ocean are subject to periodic but heavy fogs. Fog precipitates on any rise, e.g., rocks, plants and even animals.

On the morning of 13 August, 1989, a thick fog covered the Namib Desert from the coast to at least as far inland as the Desert Ecological Research Unit of Namibia at Gobabeb (60 km east of the coast). At 0800 hours, a large (> 80 mm length) *Parabuthus villosus* (Peters) was observed 15 cm above the ground on grass at Swartbank, ~40 km SE of Walvis Bay. The temperature was 12-15°C; consequently the scorpion was sluggish. It slowly moved its chelicerae over the grass stems. Water covered these stems and it was obvious that the scorpion was collecting and drinking water. We observed this behavior for 40 min before we left.

Desert scorpions obtain water in a variety of ways. Some scorpions drink surface water in the field (e.g., *Centruroides exilicauda* (Wood) [= *C. sculpturatus* Ewing], Hadley 1990). This behavior also is often observed in the laboratory (W. D. Sissom personal communication). Apparently many (most?) species never drink but derive all their water directly from the hemolymph of their prey or via

water of metabolism (see Hadley 1990). This is the only report of a scorpion using fog as a source of water.

Many Namib desert species imbibe precipitated fog (Seely 1978 for references). Several species of tenebrionids are perhaps the best known fog drinkers. Some of these beetles increase their catchment area by elevating their abdomens; some dig trenches that trap fog (Seely and Hamilton 1976). Other Namib desert insects, spiders, lizards and snakes are all known to drink fog. The observation that scorpions also drink precipitated fog increases the taxonomic diversity of species that practice such a behavior. This method of water acquisition is particularly important in the coastal section of the Namib desert; rainfall decreases monotonically from the east to west and the coastal section receives very little rain (< 10 mm/year). Conversely, fog precipitation decreases from west to east until it is largely unimportant > 110 km inland. Up to 161 mm of fog water precipitates annually near the coast.

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MATING BY FEMALE SCORPIONS WHILE STILL CARRYING YOUNG

Mating and courtship behavior are reported for 29 species of scorpion in six of the nine families of extant scorpions (Polis and Sissom 1990). However, recently post-partum females from only a few species were reported to court during the period (1-51 days) that they carry their newly born young (e.g., *Centruroides*, *Isometrus* and *Tityus* spp). All these species are in the family Buthidae, a taxon that is quite different in phylogeny, life history and behavior from scorpions in the other eight families (Polis 1990; Sissom 1990). Here, we report a courtship by *Vaejovis eusthenura* (Wood), a species of Vaejovidae in which a post-partum female mated while still carrying her young.

The mating occurred at 2330 hours on June 9, 1989 and was located 20 km east of Cabo San Lucas, Baja California del Sur, Mexico. The male and female were observed under ultraviolet light. When first observed, the male was leading the female in the courtship dance (promenade) by grasping her pedipalp chelae fingers with his own. She was carrying 14 first instars (only first instar scorpions do not fluoresce under UV). This indicates that birth had occurred within 7-17 days, the period that vaejovids (9 species reported in the literature) are known to spend before their first molt. The pair moved together for about 12 min before the male deposited a spermatophore on a small rock. He subsequently pulled the female over the spermatophore. She arched over and descended upon the spermatophore, presumably aspirating the sperm into her gonopore. Thus the mating was apparently successful. They separated immediately after the female descended on the spermatophore (See Polis and Farley 1979, and Polis and Sissom 1990 for a full description of courtship).

Since scorpions are iteroparous, courtship by post-partum females is not surprising and has been reported previously for several species (Polis and Sissom 1990). However, courtship so soon after birth has not been reported for non-buthid scorpions. Such behavior may be common but simply unobserved. This is particularly plausible in sub-tropical and temperate scorpions because the general periods of courtship (May through October in the northern hemisphere) and birth (June through September) overlap. Nevertheless, the described behavior by recent post-partum females is the first in approximately 40 observed courtship of vaejovids (*Vaejovis*, *Vejovoidus*, *Paruroctonus*), and Iurids (*Hadrurus*) that we have observed in the field.

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